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**Land cover change and biodiversity in Porto, Portugal:** a new approach to the planning of urban green infrastructures

**Filipa Guilherme**

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Department of Geosciences, Environment and Spatial Plannings
Faculty of Sciences of the University of Porto
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*To my children.*

# Foreword | Nota prévia

Under the terms of the General Regulation of the Third Cycle of Higher Education (Doctoral Programs) of the University of Porto (no. 2, article 4) and the Decree-Law 74/2006 of March 24th (article 31), revised in the Decree-Law 230/2009 of September 14th, this thesis is comprised of a collection of research articles published or submitted for publication in international peer-reviewed scientific journals, which integrate some of its chapters. Since these articles result from a collaboration with other authors, the candidate declares that she was the main responsible for the conception, data collection, analysis and discussion of results, and writing of the manuscript in its published form.

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The research work presented in this thesis was developed in the Research Centre in Biodiversity and Genetic Resources (CIBIO), an associate laboratory of the Research Network in Biodiversity and Evolutionary Biology (InBIO), and at the Faculty of Sciences of the University of Porto, under the supervision of Professor Paulo Farinha Marques and Professor Miguel A. Carretero.

Na elaboração desta tese, e nos termos do número 2 do Artigo 4.º do Regulamento Geral dos Terceiros Ciclos de Estudos da Universidade do Porto e do Artigo 31.º do D.L. 74/2006, de 24 de Março, com a nova redação introduzida pelo D.L. 230/2009, de 14 de Setembro, foi efetuado o aproveitamento de um conjunto coerente de trabalhos de investigação publicados ou submetidos para publicação em revistas internacionais indexadas e com arbitragem científica, os quais integram alguns dos capítulos da presente tese. Uma vez que os referidos trabalhos foram realizados com a colaboração de outros autores, a candidata declara que foi a principal responsável na conceção, obtenção, análise e discussão de resultados, e na elaboração da forma publicada destes trabalhos.

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# Abstract

With the global surge in human population and the consequent growth in land consumption for urbanisation, vegetation cover, habitats, and biodiversity become increasingly significant as the main providers of ecosystem services in urban areas, ultimately impacting human health and quality of life. Acknowledging the complex and dynamic character of cities, this thesis explores the urban ecosystem with a strong emphasis on its fine-scale spatial pattern and its temporal evolution. Using the city of Porto, Portugal, as a case study, this research, organised into three articles, aims to uncover the spatio-temporal patterns of land cover change and its relationship with urban biodiversity.

Initially, in the first article, a comprehensive analysis of the evolution of land cover in Porto, from 1947 to 2019, was performed at a fine scale. The results revealed an increasing trend of urban expansion and densification since the mid-20$^{th}$ century and the consequent drastic loss and fragmentation of vegetation cover, notably herbaceous habitats. The second article examines land cover trajectories for the same period to identify persistent or older habitats, i.e. habitats with a higher habitat temporal continuity. Priority areas for biodiversity conservation were then delineated, based on the assumption that habitats with a higher temporal continuity present higher biodiversity levels. Finally, in the third article, the relationship between land cover change and biodiversity was investigated, using the species richness of birds, reptiles, and amphibians as indicators. The findings highlight the significance of past land cover and its evolution in shaping urban biodiversity, as all groups seem to respond positively to older vegetation patches but negatively to long-urbanised areas. Diverse responses were also observed among the selected vertebrate groups, with birds showing greater adaptability to land cover change, whereas amphibians and reptiles have a delayed response to habitat loss and fragmentation.

Ultimately, this thesis provides useful ecological insights, methodologies, and recommendations for urban planners, designers and managers, in the scope of biodiversity conservation towards more resilient, sustainable and healthy cities.

**Keywords:** landscape change; local scale; spatial prioritization; urban dynamics; urban habitats; urban planning.

# Resumo

Com o aumento global da população humana e o consequente crescimento do consumo de solo para urbanização, o coberto vegetal, os habitats e a biodiversidade tornam-se cada vez mais significativos como os principais fornecedores de serviços de ecossistema nas áreas urbanas, influenciando a saúde humana e a qualidade de vida. Considerando o carácter complexo e dinâmico das cidades, esta tese explora o ecossistema urbano com especial ênfase no seu padrão espacial de escala fina e na sua evolução temporal. Utilizando a cidade do Porto, Portugal, como caso de estudo, esta investigação, organizada em três artigos, tem como objetivo desvendar os padrões espácio-temporais da alteração da cobertura do solo e a sua relação com a biodiversidade urbana.

Inicialmente, no primeiro artigo, foi realizada uma análise detalhada da evolução da cobertura do solo no Porto, de 1947 a 2019, a uma escala fina. Os resultados revelaram uma tendência crescente de expansão e densificação urbana desde meados do século XX e a consequente perda e fragmentação drásticas do coberto vegetal, nomeadamente dos habitats herbáceos. O segundo artigo examina as trajetórias de cobertura do solo durante o mesmo período para identificar os habitats mais persistentes ou antigos, ou seja, habitats com uma maior continuidade temporal. Foram então delineadas áreas prioritárias para a conservação da biodiversidade, com base no pressuposto de que os habitats com maior continuidade temporal apresentam níveis de biodiversidade mais elevados. Finalmente, no terceiro artigo, a relação entre a alteração da cobertura do solo e a biodiversidade foi investigada, utilizando a riqueza específica de aves, répteis e anfíbios como indicadores. Os resultados sublinham a importância da cobertura do solo no passado e da sua evolução para a estruturação da biodiversidade urbana, uma vez que todos os grupos parecem responder positivamente a manchas de vegetação mais antigas, mas negativamente a áreas urbanizadas há mais tempo. Foram também observadas respostas diversificadas entre os grupos de vertebrados selecionados, em que as aves revelam uma maior adaptabilidade à alteração da cobertura do solo, enquanto os anfíbios e os répteis parecem apresentar uma resposta demorada à perda e fragmentação do habitat.

Fundamentalmente, esta tese proporciona conhecimentos ecológicos, metodologias e recomendações úteis para os planeadores, projetistas e gestores do ambiente urbano, no âmbito da conservação da biodiversidade para cidades mais resilientes, sustentáveis e saudáveis.

**Palavras-chave:** alteração da paisagem; escala local; priorização espacial; dinâmica urbana; habitats urbanos; planeamento urbano.

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# Chapter 1.

# General introduction

## 1.1. The significance of urban biodiversity

> *"The battle for life on earth will be won or lost in urban areas."*
> - *Ahmed Djoghlaf, Former Executive Secretary of the Convention on Biological Diversity (Doyle, 2008)*

Urban biodiversity can be defined as "the variety and richness of living organisms (including genetic variation) and habitat diversity found in and on the edge of human settlements" (Müller, 2010). Contrary to what is traditionally believed, urban areas can present high levels of biodiversity, due to a myriad of factors, among which:

1) human settlements are often established in zones with rich geological and geomorphological profiles, including the presence of fresh water, river banks, sea shores, and fertile soils, which benefited not only humans but also contributed to the diversity of natural habitats (Kühn et al., 2004);
2) cities frequently present a mixed mosaic of small-scale habitats, combining remnants of natural and semi-natural habitats (e.g. forests, swamps, rivers, meadows, pastures, arable fields) with more artificial habitats that are exclusive to the urban ecosystem (e.g. walls, buildings, gardens, brownfields) (Farinha-Marques et al., 2011; Müller & Werner, 2010);
3) when compared with their surrounding environment, cities exhibit unique biophysical conditions, such as higher temperatures, altered water cycles, increased nutrient input, higher pollution levels, frequent disturbance, increased habitat fragmentation, etc., due to changes in landscape composition, configuration, and land uses (Kühn et al., 2004; Müller & Werner, 2010);
4) species assemblages that originate in the particular conditions of urban ecosystems are significantly different from the plant and animal associations and communities found in other landscapes, including a relevant proportion of non-native species, some species that only occur in urban environments, and even rare or threatened species (Gaertner et al., 2017; Ives et al., 2016; Müller & Werner, 2010).

From an ethical point of view, biodiversity should be protected due to its intrinsic value and its fundamental right to exist; from an utilitarian perspective, biodiversity should be protected since it positively contributes to the livelihood, security, health, and ultimately survival, of the human species (R. H. Haines-Young & Potschin, 2010). With urban areas

expanding globally, with more people living in cities than ever before (United Nations, 2019), the importance of biodiversity conservation in urban areas intensifies, particularly given the heightened demand for natural resources to sustain human activities in densely populated urban regions.

Urban biodiversity is essential for urban ecosystem functioning and it delivers many ecosystem services to human citizens (Harrison et al., 2014; Millennium Ecosystem Assessment, 2005; Pinho et al., 2021). Ecosystem services can be defined simply as "the benefits people obtain from ecosystems", and include: 1) provision of material goods (food, water, timber, fibre, etc.), 2) regulation of climate, floods, disease, water purification, air quality, and other ecological processes directly affecting humans, 3) cultural values, such as recreation, aesthetics, and spirituality, and 4) supporting services such as soil formation, photosynthesis, nutrient cycling, biodiversity support, and other ecological functions that promote other ecosystem services (Gómez-Baggethun et al., 2013; Millennium Ecosystem Assessment, 2005). In the specific context of urban areas, research has demonstrated that biodiversity positively affects human physical, mental and social health (Aerts et al., 2018; Cameron et al., 2020; Kilpatrick et al., 2017; Marselle et al., 2021; Schebella et al., 2019; Taylor & Hochuli, 2015; Wood et al., 2018), and enhances cities' resilience to environmental change (Campbell et al., 2009; R. M. De Carvalho & Szlafsztein, 2019; Knight et al., 2021), thus serving as a key driver of urban sustainability and quality of life for urban dwellers.

## 1.2. Biodiversity and urban landscape change

Urbanisation is a complex and dynamic phenomenon, driven by a multitude of interacting social, economic, and environmental factors (Peng et al., 2017; Ramalho & Hobbs, 2012; Shaw et al., 2020). This process gives rise to landscapes characterized by exceptional spatial and temporal heterogeneity, influencing ecological processes across various scales (Alberti et al., 2020; Mary L. Cadenasso et al., 2007). The urbanisation of landscapes implies the expansion or densification of built-up and impervious surfaces and the loss and fragmentation of vegetation cover, natural habitats, and agricultural land, whose effects vary in shape and intensity according to time and location (Güneralp et al., 2020; Richards & Belcher, 2020).

Urban landscape transformation, along with the consequent change in environmental conditions, has detrimental effects on biological communities (Aronson et al., 2014;

Concepción et al., 2016; Liang et al., 2023; Piano et al., 2020). As such, urbanisation is considered a key threat to biodiversity levels at multiple scales, with habitat loss and modification being one of the main direct drivers (N. B. Grimm et al., 2008; McDonald et al., 2020; Simkin et al., 2022; Tilman et al., 2017). Therefore, in the context of biodiversity conservation, the importance of older habitats in urban areas, i.e. habitats that are persistent in time and have experienced fewer changes, becomes more evident, as older habitats are associated with higher levels of biodiversity (Janssen et al., 2017; Nordén et al., 2014; Raduła et al., 2020). However, the relationship between habitat age or persistence and biodiversity remains relatively underexplored in urban ecosystems.

Habitat persistence, also termed temporal continuity, can affect the presence of different species over time by influencing different ecological processes. For example, the passage of time in persistent habitats allows for the accumulation of biological layers and the development of complex vegetation structures and diverse habitat niches, creating favourable conditions for a higher number of species (Janssen et al., 2017; Nordén et al., 2014). Furthermore, by inducing time-lagged responses, habitat transformation can affect the dynamics of metapopulations and metacommunities, such as dispersal, colonization, and extinction, which can lead to the phenomenon of extinction debt or immigration credit (Lira et al., 2019; Swan et al., 2021; Uroy et al., 2021). The effects of land cover change or land use legacy can also have an impact on ecosystem structure and function (Foster et al., 2003), which seems particularly relevant in highly dynamic and modified landscapes such as cities.

Species' response to land cover change, persistence and legacy depends on their life-history traits, namely their habitat specificity in different life stages, longevity, and dispersal capability (Lindenmayer et al., 2023; Lira et al., 2019). Species that are habitat specialists at any life stage, long-lived, and with restricted dispersal, tend to exhibit delayed responses (Krauss et al., 2010; Löfvenhaft et al., 2004; Sang et al., 2010). Specialist species are also more strongly associated with habitats that present a higher continuity, i.e. habitats that persist over time (Lõhmus & Liira, 2013; Nordén et al., 2014; Raduła et al., 2020), while recent habitats are more commonly occupied by generalist species that can tolerate a diverse range of conditions and disturbance (Callaghan et al., 2019; Ducatez et al., 2018). Therefore, specialist species are particularly susceptible to landscape changes derived from urbanisation and they face an increased probability of local extirpations even without any further habitat loss or degradation.

## 1.3. Urban planning for biodiversity conservation

The persistence of species and communities in a landscape is determined by **habitat availability and connectivity** in both space and time (Hanski, 1999; J.-L. Huang et al., 2020; Martensen et al., 2017; Uroy et al., 2021). Its **temporal dimension** gains a special significance in dynamic heterogeneous landscapes, such as urban areas (Ramalho & Hobbs, 2012). Here, the spatial distributions of biological communities are the result of fine-scale landscape patterns that vary according to the age and history of each site or habitat patch (Alberti et al., 2020; Alberti & Wang, 2022; M. L. Cadenasso et al., 2006; Foster et al., 2003).

Regarding habitat availability and connectivity for urban biodiversity conservation, the concept of **green infrastructure** stands out. For the purpose of this thesis, a green infrastructure is defined as a network of interconnected multifunctional green spaces, which increases their resilience and the benefits they provide (European Environment Agency, 2011). In urban areas, green infrastructures comprise all types of green (vegetated) and blue (aquatic) spaces, including natural and semi-natural, as well as built components, such as parks, gardens, forests, wetlands, green roofs, and other vegetated areas that collectively contribute to urban ecosystem functioning and provide benefits to humans through ecosystem services (Demuzere et al., 2014; European Environment Agency, 2012; Hansen et al., 2017). Boosted by European environmental policies, research on urban green infrastructures has increased in the last decade in European cities, although not always aimed primarily at urban biodiversity or habitat conservation (Butt et al., 2018; Chatzimentor et al., 2020; Matsler et al., 2021; Molné et al., 2023). Being a relatively recent topic in the literature, and with multiple definitions according to disciplinary and geographic contexts, its main principles are being gradually incorporated into urban planning strategies, where they can contribute to the conceptualisation and spatial organization of connected green spaces in urban environments (Davies & Lafortezza, 2017; Matsler et al., 2021).

While green space provision and connectivity are more frequently addressed in urban environment research and planning, green space age and history are often dismissed despite the intrinsic dynamic character of urban landscapes (Ossola, Cadenasso, et al., 2021). Understanding cities within a **temporal framework** is crucial for research, practice and management of urban ecosystems as it impacts their functioning, sustainability, and resilience (Ossola, Cadenasso, et al., 2021; Ramalho & Hobbs, 2012). In the context of biodiversity conservation, the temporal component of urban habitats can

be assessed, for example, as land cover change, site history, patch continuity, habitat age, or land-use legacy (e.g. Alberti & Wang, 2022; Gustavsson et al., 2007; Johnson et al., 2018).

The conservation of urban biodiversity is fundamental if cities want to tackle the climate emergency and achieve long-term sustainability (C.-W. Huang et al., 2018; Xie & Bulkeley, 2020), but, despite the call for action of international experts and institutions (e.g. ICLEI, 2020; Secretariat of the Convention on Biological Diversity, 2012), many cities fail to address challenges related to urban biodiversity promotion and management (Cooper et al., 2021; Wilkinson et al., 2013). The fields of landscape ecology and, notably, urban ecology hold significant potential in facilitating the exchange of knowledge between ecological research and urban planning (Opdam et al., 2013). However, there is still a **lack of ecological knowledge** on the functioning of the urban ecosystem and, frequently, the available data is inadequate to meet the requirements of urban planners, designers and managers (Jarvis & Young, 2005; Zhou et al., 2019). Moreover, this lack of data is particularly evident when considering a temporal perspective or a fine spatial scale (McDonnell & Hahs, 2013; Ossola, Cadenasso, et al., 2021; Wilkinson et al., 2013). There is, thus, an urgent need to generate **actionable knowledge** in the context of urban biodiversity conservation, i.e. knowledge that can be used to inform urban planners and developers and that can be integrated into urban planning policies towards a greener and more sustainable city (Garrard et al., 2018; Zhou et al., 2019).

Considering the heterogeneous and dynamic nature of urban ecosystems, ecological research should consider appropriate spatial and temporal scales and include spatially explicit data (Aronson et al., 2017; Borgström et al., 2006; Jarvis & Young, 2005; Opdam et al., 2013). **Spatialization**, i.e. utilizing spatial representations of ecological data, is one of the most powerful tools to enhance communication between multidisciplinary scientific groups and non-specialist decision-makers, thus aiding in the creation of actionable knowledge to guide urban planning, design, and management (Jarvis & Young, 2005; Pedersen et al., 2004). Spatial ecological data is essential for the development of **spatial prioritization** strategies regarding biodiversity conservation, allowing for the identification of critical areas, efficient allocation of resources, and optimisation of interventions for maximum impact (Jalkanen, 2020; Jalkanen et al., 2020). Spatial prioritization is fundamental in urban territories, which are highly disputed for multiple uses and functions by different stakeholders (Haaland & van den Bosch, 2015; Jalkanen et al., 2020).

The heterogeneity of the urban environment is reflected in its complex and diverse pattern of fine-scale habitats, mainly generated by anthropogenic influences (Gilbert, 1989). This means that most urban habitat dynamics occur at the site or neighbourhood level, also designated as the **local scale**, which can be defined as the physical areas that are directly intervened by urban planners, designers, managers, and users (Brown, 2017; Opdam et al., 2013). Thus, the local scale is particularly relevant for urban plans and management programs, but most fail to integrate ecological knowledge as there is insufficient availability of fine-scale data on urban ecosystems (Brown, 2017; Childers et al., 2015; Opdam, 2013). Ideally, urban planning, design, and management should also consider the **temporal** variation of the urban ecosystem, as it influences habitats and species dynamics (Ossola, Cadenasso, et al., 2021; Ramalho & Hobbs, 2012).

## 1.4. Thesis objectives and structure

The main goal of this thesis is to contribute to the planning of urban green infrastructures by identifying urban biodiversity hotspots, based on the relationship between biodiversity and land cover change. This relationship was explored using the city of Porto (Portugal) as a case study. Porto is a densely urbanized area, with very few remaining green areas, located in a temperate area, with extraordinary conditions (climatic, geologic, cultural, etc.) that originate a high biodiversity potential. The rarity of green spaces and the growing urban pressure, as well as the constrained logistic and financial resources, make Porto a good case to develop a prioritization method for urban biodiversity conservation, that could be applicable in multiple other cities facing similar challenges.

To achieve this main goal, the research was sectioned into several smaller tasks and objectives that are displayed in the different chapters of this thesis. The thesis is composed of five chapters: chapter 1 presents a general introduction to the topics of research; chapters 2 to 4 consist of the main body of research; and chapter 5 finishes this thesis with the general discussion, reflecting on the main findings and recommendations, as well as limitations and future research.

Chapter 2 presents a traditional approach to the study of land cover change in Porto, using a fine scale, from the mid-20$^{th}$ century to a recent date. Land cover patterns are assessed independently for each date and spatial metrics are used to investigate the evolution of land cover patterns. This chapter intends to demonstrate how even a simplified analysis of land cover patterns and evolution can be useful to inform spatial

planning at a fine scale, but is insufficient to determine site history, land cover legacy, or biodiversity value.

In chapter 3, a rapid method to determine the biodiversity conservation value of urban areas is proposed for situations when there is insufficient species data and experts are not available, based on the assumption that older and less disturbed habitats have higher species diversity. This chapter builds on the knowledge from the previous chapter and presents a dynamic perspective to the study of the urban territory, where the land cover history of each site is revealed on a detailed spatial and temporal scale. The city of Porto is again used as a case study for the application of the methodology, where the areas with higher habitat temporal continuity are identified after the assessment of land cover trajectories.

Chapter 4 investigates how the evolution of land cover influences biodiversity, using species richness of selected vertebrate groups, highly different in life-history and dispersal, as indicators of biodiversity levels. The detailed assessment of land cover evolution performed in the previous chapter worked as a foundation to explore the relationship between biodiversity levels and land cover change and legacy. This allowed testing the assumption that areas with higher habitat continuity have higher levels of biodiversity, as the areas with greater species richness were identified through a modelling framework, for the case of Porto.

Chapters 2, 3 and 4 were written in the form of research articles, developed exclusively in the context of this doctoral research, and were published in scientific journals. For this reason, each chapter includes its own introductory section, characterization of the study area, description of data and methodological procedures, explanation of results, discussion and conclusions. The need for these chapters to function as stand-alone manuscripts generates some unavoidable repetition of information, especially regarding some theoretical concepts and information on the study area. Some minor formatting changes were made to the original manuscripts while organizing these chapters to obtain a coherent thesis outline (e.g. numbering and positioning of figures and tables, referencing style, language form). Details of each publication are given at the beginning of each chapter and the original published articles are provided in the Appendices.

# Chapter 2.

# Looking closer at the patterns of land cover in the city of Porto, Portugal, between 1947 and 2019 – a contribution for the integration of ecological data in spatial planning

Published as a **research article** in ***Land*** (original publication in Appendices, Article I).

**Guilherme, F.**, Moreno, E.G., Gonçalves, J.A., Carretero, M.A., & Farinha-Marques, P. (2022). Looking closer at the patterns of land cover in the city of Porto, Portugal, between 1947 and 2019 – a contribution for the integration of ecological data in spatial planning. *Land*, *11*, 1828. https://doi.org/10.3390/land11101828

Author's contributions: F. Guilherme was responsible for the conceptualisation, development of methodology, data collection and analysis, design of graphic material, literature research, and writing.

## 2.1. Abstract

As more people reside in cities and metropolitan areas, urban vegetation assumes an increasingly important role as one of the main providers of ecosystem services in close proximity to human agglomerations. To improve the conditions for citizens and to optimise the sustainability of urban areas, the fields of landscape and urban ecology need to address the urgent priority to integrate ecological data in spatial planning, design, and management programs. With the objective to produce "actionable knowledge" for urban planning in the city of Porto (Portugal), we analyse the evolution of land cover since the mid-20$^{th}$ century at a fine spatial scale. Porto has followed the global trends of urbanisation, marked by a general increase in built-up and impervious surfaces that conquered the previously rural surrounding areas. This caused a severe decline in vegetation cover (especially herbaceous), as well as an increase in fragmentation and isolation of the remaining vegetation patches. These outcomes provide a detailed analysis of the city spatial dynamics, generating valuable information that can be relevant for future interventions regarding urban landscape change at a local scale, the most relevant for planning.

**Keywords:** landscape change; urban dynamics; spatial metrics; urban habitats; UrHBA.

## 2.2. Introduction

The concept of landscape is complex and manifold, having been appropriated by numerous disciplines, from the arts and humanities to the natural sciences (Doherty & Waldheim, 2016; Forman & Godron, 1981; Simensen et al., 2018). For the purpose of this study, landscape is "an area, as perceived by people, whose character is the result of the action and interaction of natural and/or human factors" (Council of Europe, 2000). The landscape is inherently complex, heterogenous, and dynamic (Forman & Godron, 1981; Naveh, 2012; Risser, 1987) and it requires a strong simplification into smaller spatial units to be comprehensively analysed (Bunce et al., 1996; Simensen et al., 2018). The landscape is characterised not only by the physical attributes of the land but also the human experience of it, i.e., by its composition, pattern, and relationship between its components, as well as the perception of all these factors (Kaplan, 1985; Naveh, 2012).

Urbanisation is one of the main generators of change in landscape patterns and composition, as it generally implies the spread and/or densification of built-up and impervious surfaces and the loss and fragmentation of vegetation, natural habitats, and agricultural land (Güneralp et al., 2020; Richards & Belcher, 2020). This, in turn, negatively affects the biodiversity levels (Beninde et al., 2015; Norton et al., 2016; Rastandeh et al., 2017), environmental conditions (R. M. De Carvalho & Szlafsztein, 2019; Gatto et al., 2020; Grigoraș & Urițescu, 2019; Kafy et al., 2022; Y. Liu et al., 2018; Melaas et al., 2016) and quality of life in urban areas (Dobbs et al., 2017; Mears et al., 2019; Wei et al., 2017). Particularly in urban environments, vegetation can be considered one of the most important contributors to environmental conditions, impacting the regulation of temperature, mitigation of flooding episodes, carbon sequestration and storage, adsorption of pollutants, provision of habitats for biodiversity, and supply of green spaces for recreation (R. M. De Carvalho & Szlafsztein, 2019; Dobbs et al., 2017; Robinson & Lundholm, 2012; Smith et al., 2017).

Cities and metropolitan areas are becoming more and more important in the context of the evolution of the human global population. In the mid-20$^{th}$ century, urban areas were populated by only around 30% of the global population (0.75 billion people); nowadays, around 55% of all humans live in urban settlements (4.22 billion people), as reported by the United Nations (United Nations, 2019). In 2050, it is estimated that around 68% of the world's people will be urban dwellers (6.68 billion)—in fact, it is expected that all of the future growth in world population will be located in urban areas (United Nations, 2019).

In the face of the rise in urban population, the Sustainable Development Goals of the United Nations highlight the need to pursue sustainability in urban centres, through the creation or transformation of cities so that they are greener, less polluted, and more resilient to climate change, ecological invasions, and emergent diseases, in order to increase the health and quality of life of their citizens and minimise the effects of natural disasters (Gaertner et al., 2017; Riley, 2021; United Nations, 2020). To achieve sustainable cities, the discipline of Landscape Ecology can play a central role in the multidirectional transfer of knowledge between ecological research and urban planning (Opdam et al., 2013). However, when compared to their natural counterparts, urban ecosystems generally present a very complex, heterogeneous, and dynamic landscape, driven by a multitude of interacting social, economic, and environmental factors, which translates into additional challenges for spatial planning and management (Borgström et al., 2006). Furthermore, there is often a mismatch of temporal and spatial scales, where

the time and land units for planning and management decisions do not coincide with the ecological processes (Borgström et al., 2006; Opdam et al., 2013). These factors can introduce barriers to the "knowledge to action" process, where both ecological research and policies at a broad scale (international or national level) are difficult to translate to the local level (Childers et al., 2014, 2015; Opdam et al., 2013). The "local level" can be defined as the physical areas that are directly intervened by urban planners, designers, managers, and users (Opdam et al., 2013). In urban contexts, the ecological dynamics of the landscape are largely affected by local scale decisions such as the planning and design of individual sites, infrastructures, and community masterplans (Brown, 2017). At the local level, historical data about the environmental conditions of each site can also present important ecological opportunities and constraints; for example, historic ecological data often serve as an inspiration for urban design and landscape architecture projects, regarding ecosystem performance and aesthetic expression (Brown, 2017).

Most ecological research is focused on the advancement of academic knowledge, intended to inform policies at a broad scale, but with limited value for landscape planning at the city or neighbourhood level. Accordingly, most spatial planning and management programs fail to integrate ecological data (Brown, 2017; Childers et al., 2015; Opdam, 2013). Thus, it is imperative that scientists, planners, designers, communities, and other local stakeholders work collaboratively, creating and transferring knowledge in a format that is clear and useful for every thematic field, in an effort to advance the field of sustainable landscape planning (Brunet et al., 2018; Childers et al., 2014, 2015; Pauleit et al., 2020; Pickett et al., 2016).

In highly heterogeneous and dynamic regions, such as urban areas, ecological research must adapt a fine spatial scale and seek detailed temporal information that can be complemented with diverse social, economic, cultural, and political data, which are crucial to inform landscape planning and design, adjusted to the local context of each city (Brown, 2017; Opdam et al., 2013). In this sense, the study of land cover facilitates the quantitative analysis of the spatial patterns of vegetation and acts as a proxy for habitat distribution (Dobbs et al., 2017). Land cover can be defined as the physical material that covers the surface of the landscape, usually related to vegetation types or artificial structures (R. Haines-Young, 2009). The concept of land cover is easily applicable everywhere as it transcends local conditions (Farinha-Marques et al., 2017), but on the other hand, it is relevant at a local scale as it can be directly transformed through most urban interventions, not necessarily requiring a change in land use type. In contrast, land use classification, often used in urban ecological studies, is difficult to

associate with biodiversity, habitat, and environmental conditions, as the relationship with vegetation cover remains unclear.

These challenges seem to be particularly relevant in compact cities (Bibri et al., 2020; Haaland & van den Bosch, 2015; Jim et al., 2018; Wolff & Haase, 2019). As these undergo processes of densification, adequate policies regarding sustainable urban planning, advocating for habitat and biodiversity conservation while offering a suitable quality of life for residents, become imperative as there is (literally) no room for error. In this urban context, there is a pressing need for a concerted effort between multiple disciplines and professionals to generate useful knowledge, closer to the scale of intervention, in order to come up with innovative and tailor-made actions fitted to the local context.

With this in mind and using a compact city from the temperate region as a case study (Porto, Portugal), we analysed the change in urban land cover for an approximate period of 70 years. Our general intention was to produce "actionable knowledge" (Brunet et al., 2018) with a fine spatial scale and vast temporal span. Thus, our research objectives were to (1) assess the land cover of Porto for three representative dates encompassing the main landscape changes, from the mid-20$^{th}$ century to recent days; (2) analyse the evolution of landscape pattern and composition with spatial metrics; and (3) identify the main trends, at a small scale, that could inform local plans and support direct actions taken by local governance and management systems for a more sustainable city.

## 2.3. Methods

### *2.3.1. Study area*

This study focuses on the Municipality of Porto, Portugal, in Southwestern Europe (Figure 2.1). The city is located in Northern Portugal, at the intersection of the Douro River with the Atlantic Ocean, where the temperate climate, with mild temperatures year-round and higher precipitation in the winter (Csb regime, according to the Koppen–Geiger classification system; Peel et al., 2007), benefits a diverse community of plant species and habitats for European standards. The latest climate records indicate a mean annual temperature of 15.3 °C and total annual precipitation of 1174.0 mm (data for 2021; PORDATA, 2022).

The region has been occupied since pre-historic times, but it remained a small and compact urban centre, surrounded by agriculture and forest, until the 19th century. In contrast, the industrial development in the 20th century boosted the expansion of the built-up area to its administrative limits, forming an urban continuum with the adjoining municipalities (Ramos, 2000). Despite its limited size (around 42 km$^2$ and almost 232,000 inhabitants; INE, 2022), Porto is currently the dynamic core of a metropolitan area composed of 17 municipalities, housing 1.7 million residents (AMP, 2022).

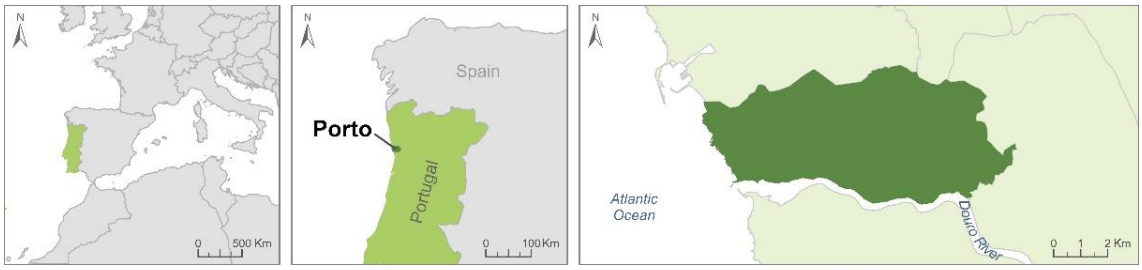



**Figure 2.1.** Location of the city of Porto, Portugal.

### *2.3.2. Land cover mapping and classification*

One of the main purposes of this study was to quantify the change in land cover of Porto considering a substantial time interval, based on historic remote sensing data. With this in mind, we decided to use three moments in time: one for the present time, one for a distant past (going as far back as possible with reliable data), and one intermediate moment. As far as our knowledge goes, the oldest aerial photography covering the city of Porto dates back to 1939, and it is available for consultation in the archives of the municipality. However, that first survey had substantial gaps, not covering the entire territory, and was executed during the winter, which makes it difficult to record deciduous vegetation; for these reasons, the aerial photograph of 1939 was not used for this study. The next oldest record corresponds to the 1947 photography obtained from Centro de Informação Geoespacial do Exército. The recent records of land cover in Porto were analysed based on the 2019 satellite photography, accessed through Google Earth. For the intermediate moment, considering similar intervals from the first and to the last moment, the 1979 aerial photography was selected, and it was made available for this study through a collaboration with the Municipality of Porto. Thus, the land cover for the city of Porto was analysed, through the interpretation of aerial and satellite imagery, in

vectorial format in GIS software (ArcMap Desktop 10.5) for three different years: 1947, 1979, and 2019.

In order to have aerial photos as georeferenced raster layers in a GIS, original images must be orthorectified (Gonçalves, 2016; Pinto et al., 2019). In the case of historical photos, this task may pose several difficulties due to the lack of knowledge about technical aspects of the aerial cameras used and also due to the difficulty in finding common points to present time images for a proper image georeferencing. Pinto et al. (2019) propose a methodology based on individual photos, requiring a minimum number of 6 ground control points (GCPs) per photo. In the case of the 1947 photos, in a total of 24, finding the required number of GCPs would be difficult due to the changes that occurred in the city. Another methodology, proposed by Gonçalves (2016), applicable to a standard coverage of aerial photographs with 60% overlap, requires a minimum of 4 points to georeference a block of images. It makes use of the structure from motion (SfM) strategy, now largely used for orthorectifying images acquired by drones. The method was applied with the Agisoft Metashape program (Gonçalves, 2016). It starts with the application of computer vision algorithms to find common points between overlapping images, generates a point cloud and a 3D model of the terrain, which is georeferenced in a block by a set of GCPs that perform 3D translation, rotation, and scale. Figure 2.2.a-b represents a typical GCP in a garden that kept its original shape in the 1947 photo and in present time orthoimages. A set of 6 GCPs were used, resulting in residuals which can be used as a quality control of the georeferencing process. A root mean square error smaller than 2 m was obtained, which was considered appropriate for the analysis to be carried out. This is followed by a set of additional processing steps, resulting in a final orthomosaic, which can be inserted in the GIS and overlaid with other georeferenced data. Figure 2.2.c shows a sample of the orthomosaic with vector polygons of building blocks. The quality of the orthomosaic geolocation was considered appropriate for a precise combination with other GIS data layers.

Land cover was classified with a version of the UrHBA method (Farinha-Marques et al., 2017), streamlined for exclusive use with remote sensing data, especially considering the low resolution and black/white colour of the older photographs. UrHBA is a spatially explicit method, based on the visual interpretation of the landscape, designed to describe urban environments in a fine scale, making it particularly oriented for scientific research, urban planning, and data communication. Unlike traditional classifications of urban land that rely on land use data, UrHBA is based exclusively on land cover, which has a direct relationship with the presence or absence of vegetation. The classification of land units

based on life traits of vegetation (instead of species or botanical communities) makes the method easily applicable in a wide range of geographical contexts. If necessary, the method allows for a more thorough characterisation later on, with the addition of detailed attributes, which should be obtained through fieldwork. The land cover categories used in this study are (1) Artificial Built Elements, ABE; (2) Trees and Shrubs, TRS; (3) Herbaceous, HER; (4) Sparsely Vegetated - Terrestrial, SPV; and (5) Sparsely Vegetated - Aquatic, AQU (Table 2.1). These were adapted from Urban Habitat Categories and super-categories from UrBHA (for further detail and definition of the categories, see Farinha-Marques et al., 2015, 2017). The mapping procedure was also simplified—all elements were mapped as patches, even if with a linear shape; the minimum dimension for patches to be distinguished was 2000 $m^2$, and the minimum width was 5 m.




**Figure 2.2.** (a) Examples of a GCP in the 1947 aerial photo; (b) the same point in present time orthoimages; (c) large portion of the final orthomosaic, with overlaid vector data of building blocks in a GIS, showing the accurate geolocation of the orthomosaic.

**Table 2.1.** Land cover categories (adapted from Farinha-Marques et al., 2017).

| Land cover categories | Abbreviation | Description |
|---|---|---|
| Artificial Built Elements | ABE | Impervious surfaces, buildings, and other constructed elements. |
| Trees and Shrubs | TRS | Woody vegetation, including all phanerophytes and shrubby chamaephytes. |
| Herbaceous | HER | Herbaceous vegetation, including hemicryptophytes, therophytes and geophytes. |
| Sparsely Vegetated - Terrestrial | SPV | Every type of non-vegetated soil, such as bare soil, sand, and rock. |
| Sparsely Vegetated - Aquatic | AQU | Every type of water surface, such as the sea, rivers, lakes, and ponds (including artificial elements). |

### *2.3.3. Spatial metrics*

Land cover patterns were monitored by means of spatial metrics, which can be used as indicators of habitat availability, shape, fragmentation, and connectivity. For the purpose of the generation of spatial metrics, the term “patch” corresponds to the smaller spatial unit with homogeneous land cover, “class” consists of the group of all patches with the same land cover, and “landscape” identifies the entire study area, formed by a heterogeneous mosaic of patches (McGarigal, 2015).

Spatial metrics were calculated with V-LATE 2.0 beta (Lang & Tiede, 2003) for the three resulting maps of land cover classification, at landscape, class, and patch levels. For landscape-level analysis, all patches are considered for the calculations, i.e., all the different land cover categories are included in the same analysis; at the class-level analysis, individual calculations are performed for each land cover category; and at patch-level, a series of metrics is generated for each land cover patch. This software uses vectorial data for the calculation of the most common metrics, and a few were selected as indicators of composition and configuration of the urban landscape, as shown in Table 2.2. These metrics can be grouped as (1) area and edge metrics - fundamentally related to the basic dimensions of patches, such as area and perimeter, and important for the analysis of habitat availability, fragmentation, and edge effects; (2) shape metrics - related to patch morphology and geometric complexity, which can influence edge effects, animal migration, and plant colonisation processes; (3) aggregation metrics - these indicate the tendency of patch types to be more or less dispersed and separated in the landscape, also known as “landscape texture”, influencing a diverse array of ecological processes, especially those concerning habitat loss, fragmentation, and isolation; (4) diversity metrics - important to understand the landscape composition, and only calculated for the landscape level of analysis (McGarigal, 2015).

Finally, a Kruskal-Wallis test was performed on SPSS Statistics v.27 software to check for significant differences between patch metrics for the three moments. The Kruskal-Wallis test is a nonparametric method for testing if multiple groups follow the same distribution. Next, a *post hoc* Dunn’s test was used for pairwise comparisons, in the case of rejection in the Kruskal-Wallis test, to identify which date shows a significant difference. These results were then interpreted considering the landscape as a whole and for each individual land cover class and thus are presented together with the landscape- and class-level analyses.

**Table 2.2.** Landscape metrics selected for this study (adapted from Lang & Tiede, 2003; McGarigal, 2015).

| Level | Type | Metric |
|---|---|---|
| Landscape | Area and edge metrics | TA: Total area (ha) |
| | | LPI: Largest patch index (%) |
| | | MPS: Mean patch size (ha) |
| | | MPE: Mean patch edge (m) |
| | | ED: Edge density (m/ha) |
| | Shape metrics | MPAR: Mean perimeter–area ratio |
| | | MSI: Mean shape index |
| | | MFD: Mean fractal dimension |
| | Aggregation metrics | NP: Number of patches |
| | | MENND: Mean Euclidean nearest neighbour distance (m) |
| | | MPROX: Mean proximity index |
| | Diversity metrics | CR: Class richness |
| | | SHDI: Shannon's diversity index |
| | | SHEI: Shannon's evenness index |
| Class | Area and edge metrics | CA: Total class area (ha) |
| | | CP: Class proportion (%) |
| | | LPI: Largest patch index (%) |
| | | MPS: Mean patch size (ha) |
| | | MPE: Mean patch edge (m) |
| | | ED: Edge density (m/ha) |
| | Shape metrics | MPAR: Mean perimeter–area ratio |
| | | MSI: Mean shape index |
| | | MFD: Mean fractal dimension |
| | Aggregation metrics | NP: Number of patches |
| | | MENND: Mean Euclidean nearest neighbour distance (m) |
| | | MPROX: Mean proximity index |
| | | DIV: Division index |
| Patch | Area and edge metrics | Area (ha) |
| | | Edge (m) |
| | Shape metrics | Perimeter–area ratio |
| | | Shape index |
| | | Fractal dimension |
| | Aggregation metrics | Euclidean nearest neighbour distance (m) |
| | | Proximity index |

## 2.4. Results

### *2.4.1. Land cover*

Between 1947 and 2019, the city of Porto experienced an overall trend of an increase in artificial areas, at the expense of vegetated areas (Figures 2.3 and 2.4). In 1947, the municipality of Porto exhibited two key urban areas, represented here as agglomerations of the land cover class of Artificial Built Elements (ABE): a smaller one, in the southwest, near the estuary of Douro River, and the main urban core, in a more central-southern position. These built-up areas have greatly expanded throughout the years, resulting in the duplication of the urban surface (from 31% in 1947 to 62% in 2019), currently forming an almost continuous mesh. The stability in the number of patches of ABE, along with the substantial increase in the proportion of the landscape (Figure 2.3), indicates that no new separate urban areas were created, but rather the existing ones were enlarged.

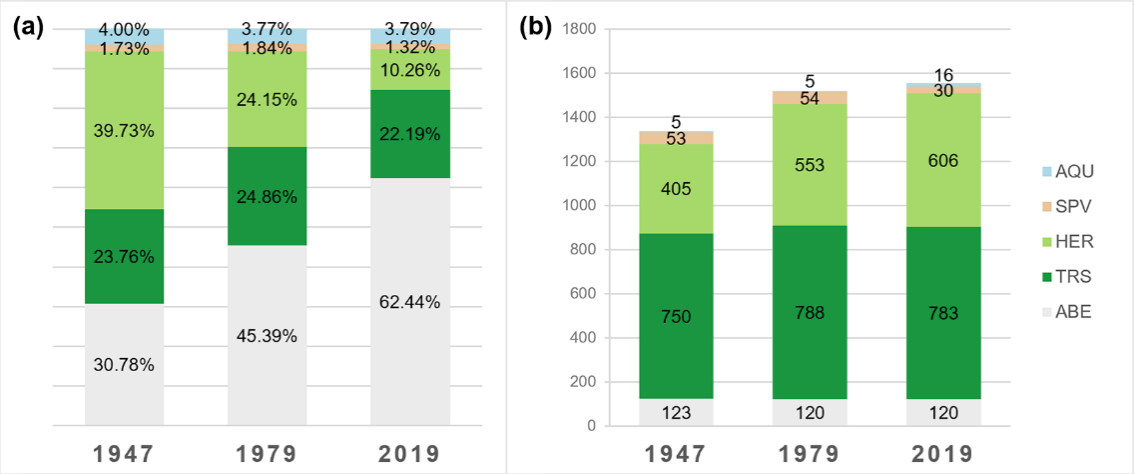



**Figure 2.3.** (a) Land cover class proportions in 1947, 1979, and 2019; (b) number of patches per class in 1947, 1979, and 2019 (see also Table 2.7).

Large patches of arboreal vegetation exist mainly in the peripheral areas of Porto, especially in the western and eastern extremes, with most of them being preserved since the mid-20$^{th}$ century (Figure 2.4). This caused the percentage of woody vegetation (TRS) within the city, as well as the number of patches, to remain virtually unchanged from 1947 to 2019 (between 22% and 25% cover, and between 750 and 783 patches; Figure 2.3). On the other hand, the city has experienced a drastic change in the proportion of herbaceous cover (HER): in 1947, the landscape was clearly dominated by herbaceous vegetation, with approximately 40% cover, which reduced to 10% in 2019 (Figures 2.3 and 2.4). Through visual analysis of the land cover maps, but mainly by means of the interpretation of the increase in the number of patches, accompanied by the reduction in

the percentage cover, it becomes clear that herbaceous habitats were the most affected in terms of availability and connectivity.

Although the classes of Sparsely Vegetated - Terrestrial (SPV) and Sparsely Vegetated - Aquatic (AQU) are considered as components of ecologically significant habitats, they have remained consistent through the time period 1947-2019 and are residual in this study area (always less than 5%; Figure 2.3). Thus, SPV and AQU will not be analysed in detail as they play a reduced role in the interpretation of land cover evolution in the city of Porto.

### *2.4.2. Spatial metrics*

#### ***2.4.2.1. Landscape-level analysis***

At the landscape level, the overall perspective of spatial metrics seems to point to a general trend of increased complexity and fragmentation (Figure 2.5; see also Table 2.7). Although the analysed study area remains the same for every year, the number of patches (NP) has increased over time, resulting in the decline of mean patch size (MPS). The increase in mean patch edge (MPE) and edge density (ED), as well as in all shape metrics (mean perimeter-area ratio: MPAR, mean shape index: MSI, and mean fractal dimension: MFD), reveal a general increase in patch shape irregularity and intricacy.

The values of mean Euclidean nearest neighbour distance (MENND) have increased throughout the analysed period, pointing to increased fragmentation and isolation of patches. Conversely, the values of mean proximity index (MPROX) have largely increased, suggesting higher proximity to large patches of the same land cover class. These results should be examined in more detail for a clearer interpretation (see class-level results below).

The territory seems to have experienced a decline in the diversity of land cover classes, especially during the transition from 1979 to 2019, as exposed by the decreasing values of the Shannon diversity index (SHDI) and the Shannon evenness index (SHEI). This indicates that one or more classes have become increasingly dominant over other classes, which can be better understood in the class-level analysis below.

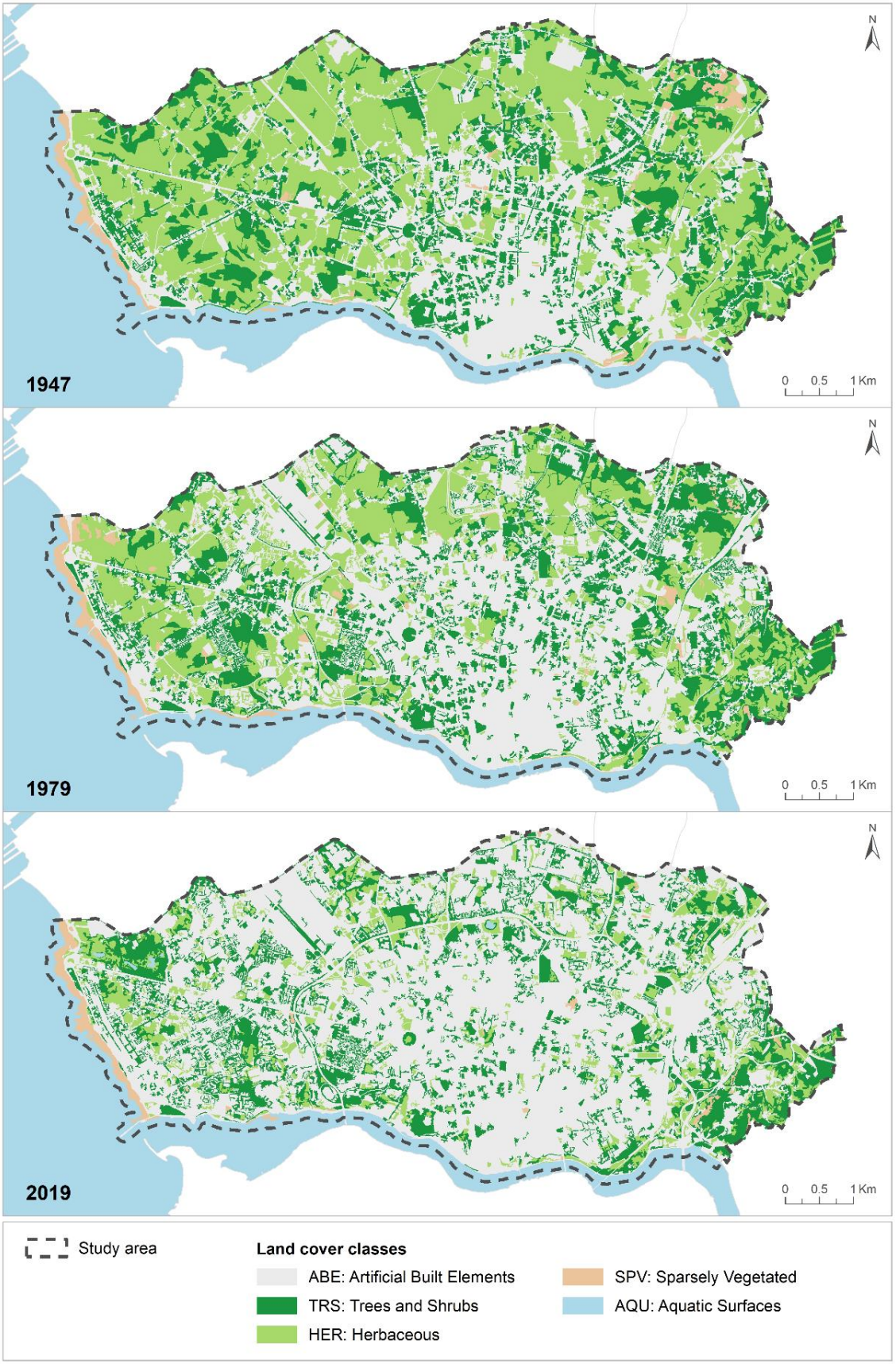



**Figure 2.4.** Land cover maps of Porto in 1947, 1979, and 2019.

Considering individual patch metrics, analysed for the entire landscape, the Kruskal-Wallis test revealed that most metrics showed significant differences for at least one of the periods; however, the mean values for Euclidean nearest neighbour distance did not differ significantly throughout the years (Table 2.3).

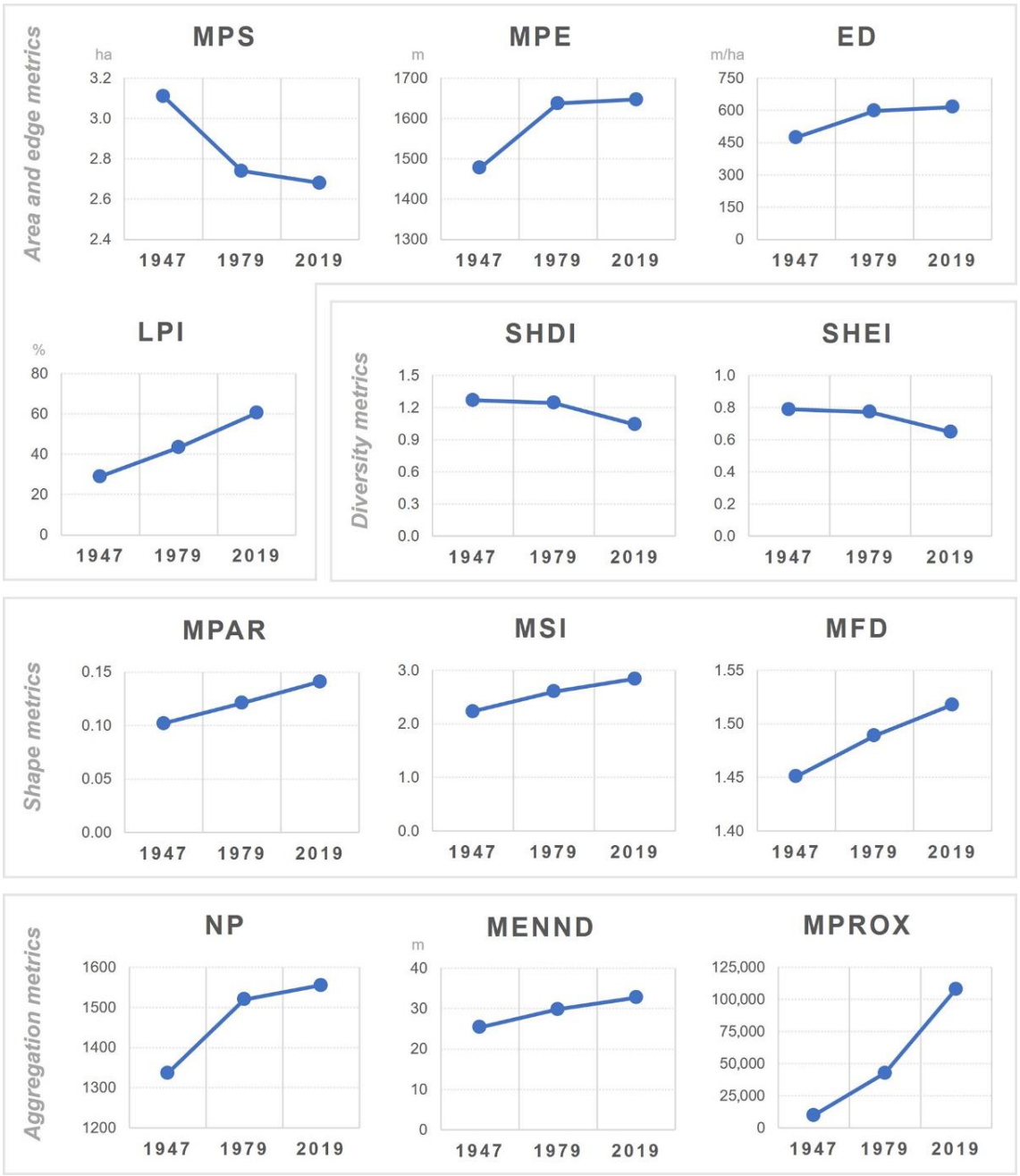



**Figure 2.5.** Evolution of spatial metrics at the landscape level, for the period 1947–1979–2019 (see Table 2.7 for detailed values). MPS: mean patch size; MPE: mean patch edge; ED: edge density; LPI: largest patch index; SHDI: Shannon's diversity index; SHEI: Shannon's evenness index; MPAR: mean perimeter–area ratio; MSI: mean shape index; MFD: mean fractal dimension; NP: number of patches; MENND: mean Euclidean nearest neighbour distance; MPROX: mean proximity index.

**Table 2.3.** Outputs of the Kruskal-Wallis test (and *post hoc* pairwise comparisons) on patch metrics, considering the analysis at the landscape level (N = 4411; significance values for Dunn's test were adjusted by the Bonferroni correction for multiple tests).

| Patch metrics | Kruskal–Wallis test | | | Dunn's test | |
|---|---|---|---|---|---|
| | Test statistic | d.f. | Sig. | Pairwise comparisons | Adj. sig. |
| Area | 53.069 | 2 | <0.001 * | 1947–1979 | 0.052 |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Edge | 18.047 | 2 | <0.001 * | 1947–1979 | 0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | 1.000 |
| Perimeter–area ratio | 403.910 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Shape index | 251.829 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Fractal dimension | 467.654 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Euclidean nearest neighbour distance | 0.803 | 2 | 0.669 | (pairwise comparisons were not performed as the overall test does not show significant differences across samples) | |
| Proximity index | 59.716 | 2 | <0.001 * | 1947–1979 | 0.020 |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |

* Significant differences.

### *2.4.2.2. Class-level analysis*

The spatial metrics for each individual class provide an overall image of increasing dominance of built-up areas (Figure 2.6; see also Tables 2.8 to 2.10). As previously explained, the results for SPV and AQU are not presented nor discussed, as their relevance in the land cover dynamics of the territory is negligible at this scale of analysis.

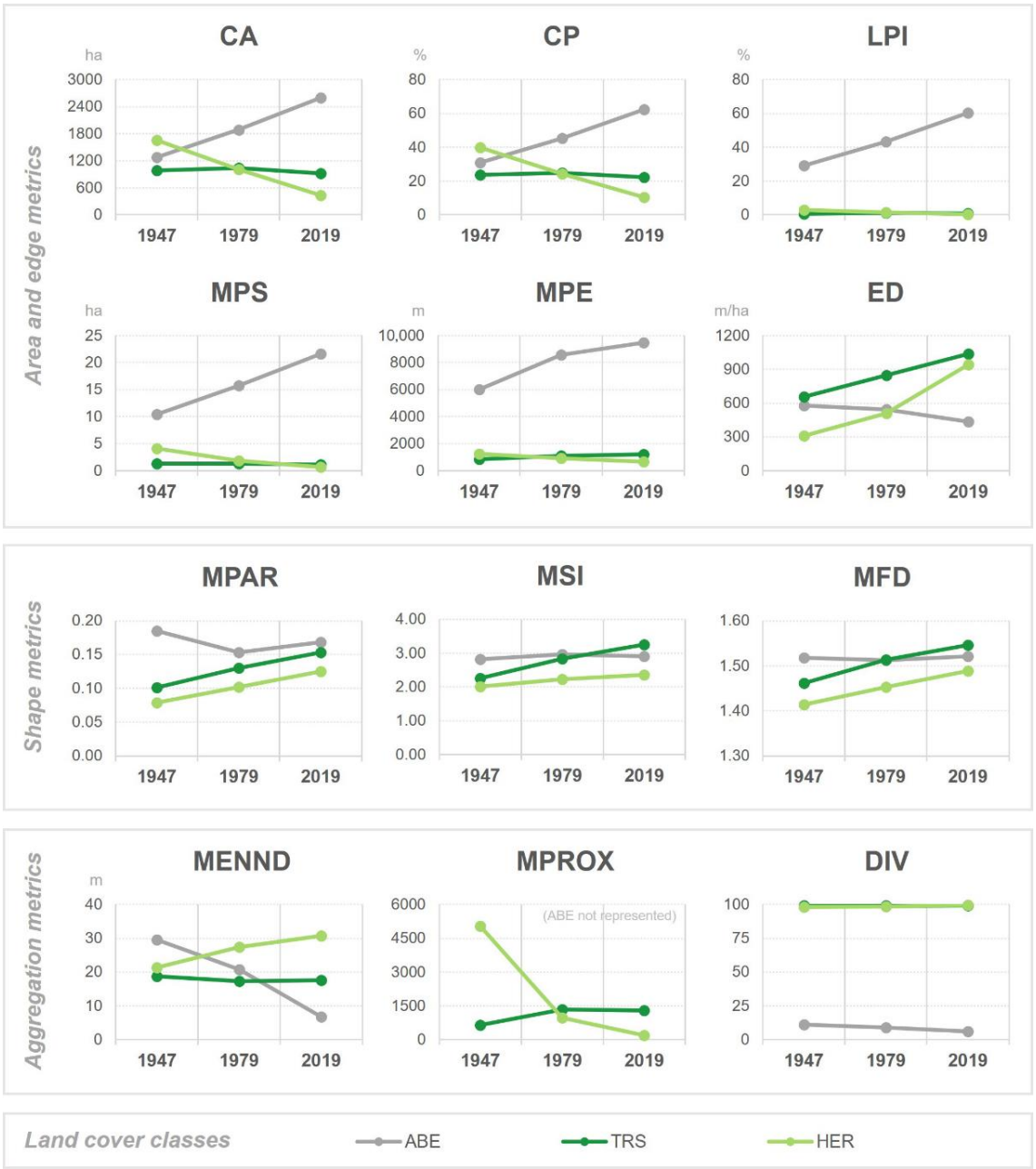



**Figure 2.6.** Evolution of spatial metrics at the class level, for the period 1947–1979–2019 (see Tables 2.8 to 2.10 for detailed values). CA: total class area; CP: class proportion; LPI: largest patch index; MPS: mean patch size; MPE: mean patch edge; ED: edge density; MPAR: mean perimeter-area ratio; MSI: mean shape index; MFD: mean fractal dimension; MENND: mean Euclidean nearest neighbour distance; MPROX: mean proximity index; DIV: division index.

**Artificial Built Elements (ABE) cover.** As expected, following the global urbanisation trends of the 20th century, the class of ABE showed a substantial increment in area, as was revealed by the area metrics: class area (CA), class proportion (CP), largest patch index (LPI), mean patch size (MPS), and mean patch edge (MPE) gradually increase

over time. Accordingly, the results in terms of aggregation metrics show a trend of decreasing MENND and increasing MPROX, which suggests higher connectivity among ABE patches over time. Shape complexity remained relatively constant throughout the years, as revealed by the evolution of shape metrics: MPAR, MSI, and MFD show similar values for the three time periods (Figure 2.6, Tables 2.8 to 2.10). Regarding the analysis of individual patch metrics for ABE land cover, the Kruskal–Wallis test revealed that most spatial metrics do not significantly differ in the three different moments, with the exception of Euclidean nearest neighbour distance and proximity index (Table 2.4).

**Table 2.4.** Outputs of the Kruskal-Wallis test (and *post hoc* pairwise comparisons) on patch metrics, considering the analysis for the ABE class (N = 363; significance values for Dunn's test were adjusted by the Bonferroni correction for multiple tests).

| Patch metrics | Kruskal-Wallis test | | | Dunn's test | |
|---|---|---|---|---|---|
| | Test statistic | d.f. | Sig. | Pairwise comparisons | Adj. sig. |
| Area | 1.019 | 2 | 0.601 | (pairwise comparisons were not performed) | |
| Edge | 3.734 | 2 | 0.155 | (pairwise comparisons were not performed) | |
| Perimeter–area ratio | 1.763 | 2 | 0.414 | (pairwise comparisons were not performed) | |
| Shape index | 1.933 | 2 | 0.380 | (pairwise comparisons were not performed) | |
| Fractal dimension | 2.426 | 2 | 0.297 | (pairwise comparisons were not performed) | |
| Euclidean nearest neighbour distance | 94.703 | 2 | <0.001 * | 1947–1979 | 0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Proximity index | 120.750 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |

* Significant differences.

**Herbaceous (HER) cover.** Area metrics (CA, CP, LPI, MPS, and MPE) reveal a severe decrease in the availability of HER land cover, while the increasing values of ED, as well as MPAR, MSI, and MFD, seem to point to a situation of increased patch shape complexity and irregularity over time. The evolution of aggregation metrics also suggests a rise in isolation and fragmentation of HER patches, as can be especially seen in the results of increasing values of MENND and decreasing values of MPROX (Figure 2.6, Tables 2.8 to 2.10). According to the Kruskal-Wallis test, all patch metrics for HER land cover class show significant differences between the analysed time periods (Table 2.5).

**Table 2.5.** Outputs of the Kruskal-Wallis test (and *post hoc* pairwise comparisons) on patch metrics, considering the analysis for the HER class (N = 1564; significance values for Dunn's test were adjusted by the Bonferroni correction for multiple tests).

| Patch metrics | Kruskal–Wallis test | | | Dunn's test | |
|---|---|---|---|---|---|
| | Test statistic | d.f. | Sig. | Pairwise comparisons | Adj. sig. |
| Area | 87.608 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Edge | 6.621 | 2 | 0.036 * | 1947–1979 | 1.000 |
| | | | | 1947–2019 | 0.044 * |
| | | | | 1979–2019 | 0.212 |
| Perimeter-area ratio | 236.792 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Shape index | 63.766 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Fractal dimension | 221.490 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Euclidean nearest neighbour distance | 33.985 | 2 | <0.001 * | 1947–1979 | 0.028 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | 0.002 * |
| Proximity index | 59.716 | 2 | <0.001 * | 1947–1979 | 0.020 |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |

* Significant differences.

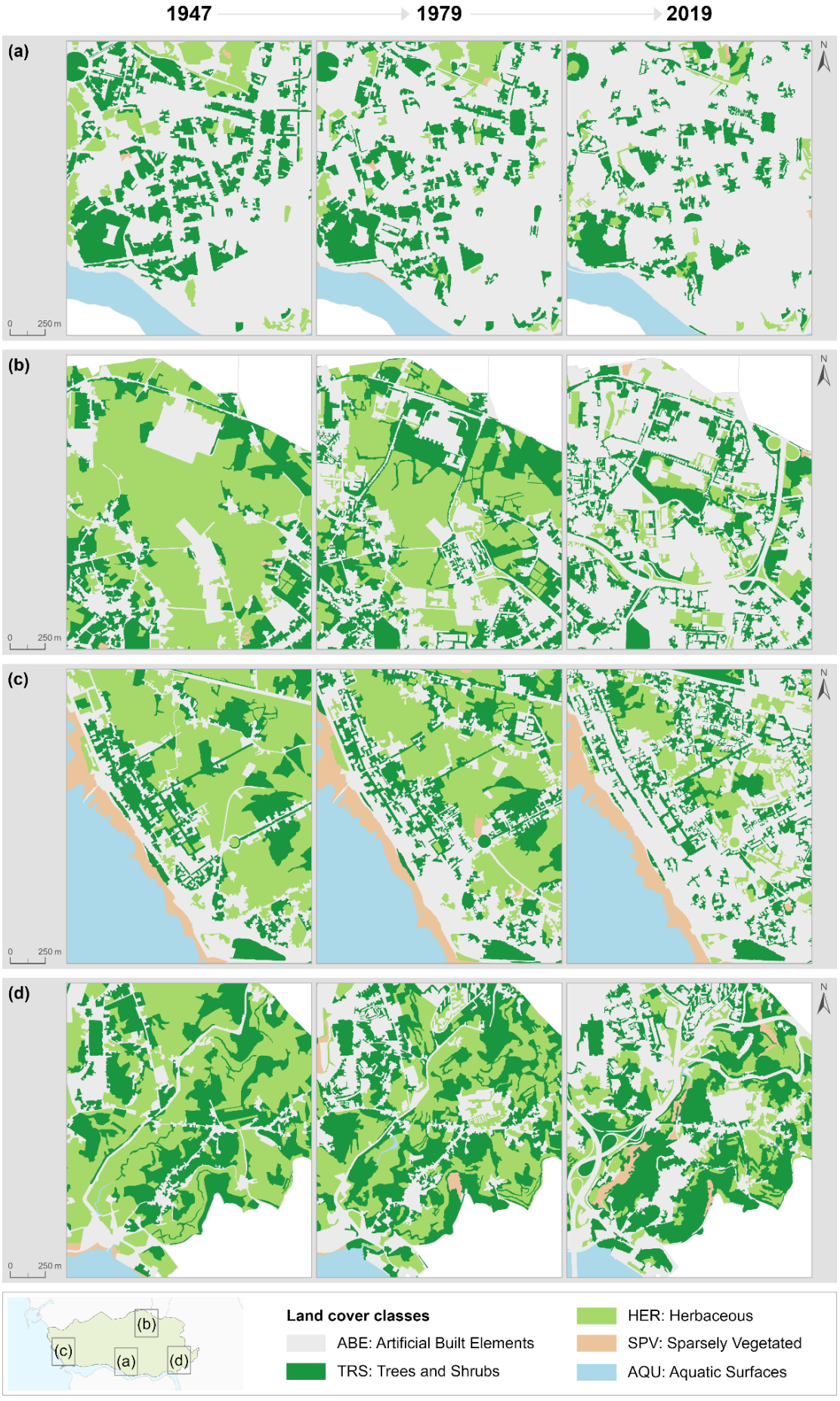
**Trees and Shrubs (TRS) cover.** According to most area metrics (CA, CP, LPI, MPS), the land cover dominated by TRS apparently maintained a fairly constant area throughout the years. The evolution of aggregation metrics (NP, MENND, MPROX, and division index, DIV) also suggests the higher stability of this land cover type regarding availability and connectivity. However, the increasing values of edge (MPE, ED) and shape metrics (MPAR, MSI, MFD) reveal a scenario of increased shape complexity and irregularity (Figure 2.6, Tables 2.8 to 2.10). Indeed, the Kruskal-Wallis test revealed that patch size and edge have significantly different values for the three analysed years, in addition to patch shape metrics (perimeter–area ratio, shape index, and fractal dimension). On the other hand, aggregation metrics for TRS have not changed significantly throughout the years (Table 2.6).

**Table 2.6.** Outputs of the Kruskal-Wallis test (and *post hoc* pairwise comparisons) on patch metrics, considering the analysis for the TRS class (N = 2321; significance values for Dunn's test were adjusted by the Bonferroni correction for multiple tests).

| Patch metrics | Kruskal–Wallis test | | | Dunn's test | |
|---|---|---|---|---|---|
| | Test statistic | d.f. | Sig. | Pairwise comparisons | Adj. sig. |
| Area | 8.280 | 2 | 0.016 * | 1947–1979 | 0.486 * |
| | | | | 1947–2019 | 0.012 * |
| | | | | 1979–2019 | 0.402 * |
| Edge | 56.523 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | 0.017 * |
| Perimeter-area ratio | 319.709 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Shape index | 302.895 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Fractal dimension | 452.896 | 2 | <0.001 * | 1947–1979 | <0.001 * |
| | | | | 1947–2019 | <0.001 * |
| | | | | 1979–2019 | <0.001 * |
| Euclidean nearest neighbour distance | 4.508 | 2 | 0.105 | (pairwise comparisons were not performed) | |
| Proximity index | 0.924 | 2 | 0.630 | (pairwise comparisons were not performed) | |

* Significant differences.

**General overview.** When analysing the city at a broad scale, there is an obvious trend of urban sprawl and densification, but this was translated with different spatial patterns in distinct portions of the city. Four main tendencies of land cover evolution were identified throughout the city, which are represented in Figure 2.7: (i) dominance of ABE from at least 1947 to the present, mostly visible in the city centre; (ii) drastic urban expansion, especially from 1979 onward, with the consequent elimination of HER cover, particularly noticeable in the northern section; (iii) slight increase in ABE surface, but with consequences in terms of increased fragmentation and irregularity of TRS and HER cover, as can be seen, for example, in the western section; and (iv) decrease in HER cover associated with increase in TRS cover, also coupled with moderate increase in ABE, as occurred in the eastern area.


1947
1979
2019
(a)
(b)
(c)
(d)
N
0
250 m
(b)
(c)
(a)
(d)
Land cover classes
ABE: Artificial Built Elements
TRS: Trees and Shrubs
HER: Herbaceous
SPV: Sparsely Vegetated
AQU: Aquatic Surfaces

▲ **Figure 2.7.** Different sections of the city, showing the main tendencies of land cover evolution: (**a**) section of the city near the centre, where ABE cover has been dominant since at least 1947; (**b**) section of the city near the northern border, that faced a significant increase in ABE cover and decrease in HER cover; (**c**) section of the city in the western extremity, where the increase in ABE cover resulted in the reduction and fragmentation of HER and TRS cover; (**d**) section of the city near the eastern limit, where HER cover was replaced by TRS and ABE cover.

## 2.5. Discussion

The city of Porto epitomises many of the urbanisation trends in vegetation cover observed in many European cities, having experienced a notorious sprawl and densification of its urban fabric in the past few decades (Kasanko et al., 2006; Pauleit et al., 2005; Richards & Belcher, 2020). In the first half of the 20th century, its territory encompassed a small city centre, as well as a few ramifications to even smaller urbanised clusters in the periphery, and was still being dominated by vegetation cover, especially herbaceous vegetation in agricultural fields. The second half of the 20th century saw an acceleration of urbanisation, and at the beginning of the 21st century, the urban fabric occupied most of the territory contained by the boundaries of Porto. The former rural areas that surrounded the historical urban centres were progressively conquered by new urbanisation processes, which caused the increased dominance of buildings and sealed surfaces (ABE cover), as well as the reduction in diversity of land cover types. Most of the herbaceous patches (HER cover) have disappeared or have been extremely fragmented and isolated from similar patches; this is mainly due to the reclamation of land for new urbanisation, but also related to the abandonment of agricultural practices. Nowadays, most of the remaining vegetation cover persists in patches of trees (TRS cover), which reveals some concern with the preservation of tree cover; in fact, while some new tree cover originated from the ecological succession in abandoned or unmanaged lots, most of the larger tree-covered patches that existed in the mid-20th century were integrated in new public parks.

These results are in line with previous studies performed for the Porto region, although for different contexts, time frames, and scales of approach. For example, in their analysis of the evolution of green spaces in Porto in the 20th century, Madureira et al. (2011) demonstrated a severe decrease in agricultural areas, accompanied by a general increase in green space destruction and fragmentation. Similarly, Bagan and Yamagata (2014) revealed an association between the urban growth of Porto and the reduction in several types of vegetation cover, within a shorter, more recent period, from 1984 to 2009. Several other cities, in Europe and worldwide, also present an urbanisation

scenario similar to that experienced by Porto in the past few decades: an increase in built-up and impervious areas and a decline in vegetation and green space cover (e.g., Gupta, 2014; Kaspersen et al., 2017; Richards & Belcher, 2020; Timalsina et al., 2021); however, it should be noted that most of these studies consider only short-term changes, rarely encompassing more than 20 or 30 years of urban land cover evolution. With a similar time frame to our study, Lennert et al. (2020) explored the past dynamics of the Budapest metropolitan region from 1959 to 2012 and obtained similar results: the growth in artificial surfaces caused the decline in vegetated areas, such as natural or agricultural land; nevertheless, the large-scale approach can make it difficult to translate to local actions in each of the individual municipalities. It is worth mentioning that a lot of cities, especially large European and North American cities, have been able to counteract this tendency of vegetation cover loss since the late 20$^{th}$ century (Corbane et al., 2020; Richards & Belcher, 2020). While some of these trends can be explained by the rise in temperatures favouring vegetation growth, many of these cities have in fact strengthened their green infrastructure and promoted the application of nature-based solutions (Zhang et al., 2021). This could also be the case of Porto if the outcomes of this study are properly integrated in urban planning.

The fine scale of analysis allows for a detailed look at specific portions of the city, which can be particularly relevant to understand the context and implications of future interventions in urban areas, which may be of significant interest for urban planners and decision makers. For example, the city centre (Figure 2.7.a) has been dominated by ABE for a long time, with a fairly constant area, and TRS cover also seems to be quite persistent. This may be suggestive of some habitat and green space conservation efforts, as most of the TRS patches that were already present in 1947 belonged to public parks, gardens, or green squares that were maintained to the present day; some private green spaces inside blocks of buildings have also been preserved. Thus, it is essential that, in this densely built area, all pervious land is protected from future construction and new opportunities for the increment of vegetation cover are seized and planned carefully to maintain appropriate levels of vegetation diversity.

On the other hand, the northern part of Porto (Figure 2.7.b) reveals an obvious scenario of rapid urban expansion where agricultural fields, dominated by HER cover, were progressively displaced by urbanisation, seemingly without much planning or conservation concerns. In this section of the city, the loss and fragmentation of vegetated areas become quite noticeable, especially due to large continuous patches of HER cover, and also TRS cover to a lesser extent, being encroached by the development of

new buildings, roads, and other infrastructures (ABE). It is recommended that future interventions in this or other areas with a similar profile take actions to preserve, enlarge, and connect the remnant patches of vegetation, in order to enhance the ecological performance of the urban ecosystem.

The western extreme of the city (Figure 2.7.c) also shows a significant decrease in the proportion of HER cover due to the decline in agricultural activities. The scenario of increase in fragmentation and shape irregularity of TRS cover is particularly visible in this portion of the city, as large patches of tree-covered private gardens and backyards, present in 1947, were gradually replaced by a denser matrix of buildings; most of the TRS patches in 2019 are tree-lined streets and narrow fragments of private gardens. In this area of the city, there are still some relatively large patches dominated by herbaceous vegetation that represent some of the few cultivated areas in the whole city that persist today. Considering the future urban developments expected for this area, we recommend that this portion of land retains the highest degree of perviousness as possible, protecting one of the few areas of the city with less disturbed soil. In this regard, we highlight two major options: (1) the preservation of agricultural spaces, for example, in the form of community gardens or allotments, and (2) the establishment of herbaceous habitats, based mainly on native plant species. These practices could contribute to the conservation of soil and water quality, while also promoting the biodiversity of grassland and farmland habitats, which is declining at the European level (European Environment Agency, 2021).

The eastern portion of Porto (Figure 2.7.d) was also dominated by HER cover in 1947, mainly in the form of crops and pastures. Although some new urban developments occurred, namely the construction of a few residential neighbourhoods and large roads, this portion remains one of the least urbanised of the city. However, the area of HER cover has also decreased substantially, especially due to the abandonment of agricultural fields, which caused an increment in mostly spontaneous TRS cover. This can pose an additional challenge due to the proliferation of invasive species that may follow the abandonment of these fields. Nevertheless, the extent of vacant land present in this portion of the city can generate opportunities for the creation of new accessible green spaces that provide numerous benefits for the urban population, especially considering the lack of public green spaces amongst this intricate urban fabric with an accentuated rural character.

Due to their higher degree of complexity and heterogeneity, the smaller scale of approach seems to be particularly relevant in urban areas, where there is a strong

competition for space among different interest groups and where decisions at a small scale can have significant ecological or social effects. For instance, decisions such as the preservation of even a small patch of vegetation can dictate the survival of a population of a certain species or can contribute to the experience of nature for the nearest residents, improving their health, well-being, and quality of life at a scale that even transcends that particular site.

To complement these results, further data could be generated encompassing, for example, a more detailed classification of vegetation types, a finer temporal scale (considering shorter time intervals), and the study of land cover trajectories. Additionally, depending on the aim of research, but particularly relevant for spatial planning, it may be worth analysing the relationship between land cover patterns and evolution with biodiversity, quality of life, health and well-being, and other factors.

As such, this research can be easily reproduced in a variety of urban areas, as the methods are quite simple and do not require prior specialised training for the visual interpretation of the landscape. However, due to the detailed scale of analysis, the method can become quite time-consuming when considering larger study areas; this could be overcome with the creation of automatic algorithms for the classification of land cover, which was outside of the scope of this research.

## 2.6. Conclusion

The city of Porto experienced evident processes of urban sprawl and densification in the last century, mimicking other cities worldwide. Thus, the findings and recommendations of this research can also be applied to a variety of cities with a similar context, particularly other European cities that are compact and undergoing phases of infill development. To counteract the loss of vegetation, especially grassland and farmland habitats, we propose that these cities invest in the conservation, restoration, or creation of herbaceous patches, in the form of meadows, allotments, urban farming, and other amenities, that could be encouraged in public and private areas. Arboreal vegetation is also important, but its conservation is a more common practice (that should be maintained). Cities that aim to be sustainable should consider several aspects regarding green spaces: maximise, to the greatest possible extent, the amount of vegetation cover in the city; enhance the diversity of green spaces and in green spaces (e.g., include different types of green spaces, with different uses and different compositions); optimise

the relation of vegetation patches with each other and with the surrounding built environment; and consider the temporal variation or continuity of vegetation.

The small-scale approach of this research brings the results closer to the scale of intervention, i.e., it allows a focus, with great detail, on particular sites, contributing to decision making in future interventions in the urban landscape (e.g., preservation of the existing vegetation, selection of the best habitats to implement, etc.). This way, the scale of approach and the emphasis on vegetation facilitate the translation of scientific research into concrete practical measures, and not just general recommendations on a broad geographic scale that are difficult to implement at the local decision scale.

This study showed that it is possible to obtain urban land cover data at a fine spatial scale, while also considering the history of the vegetation on each location. This research was outlined with urban ecology and urban planning in mind, but it can also be useful to other fields of scientific research and professional practices, such as architecture, landscape architecture, geography, social studies, etc., that take interest in improving the urban environment and the health and quality of life for urban residents.

## 2.7. Supplementary material

**Table 2.7**. Spatial metrics at the landscape level, for 1947, 1979, and 2019.

| Type | Metric | 1947 | 1979 | 2019 |
|---|---|---|---|---|
| Area and edge metrics | TA: Total area (ha) | 4160.75 | 4160.75 | 4160.75 |
| | LPI: Largest patch index (%) | 29.02 | 43.33 | 60.45 |
| | MPS: Mean patch size (ha) | 3.11 | 2.74 | 2.68 |
| | MPE: Mean patch edge (m) | 1477.24 | 1637.28 | 1646.62 |
| | ED: Edge density (m/ha) | 474.33 | 598.13 | 615.39 |
| Shape metrics | MPAR: Mean perimeter-area ratio | 0.102 | 0.121 | 0.141 |
| | MSI: Mean shape index | 2.235 | 2.604 | 2.844 |
| | MFD: Mean fractal dimension | 1.451 | 1.489 | 1.518 |
| Aggregation metrics | NP: Number of patches | 1336 | 1520 | 1555 |
| | MENND: Mean Euclidean nearest neighbour distance (m) | 25.40 | 29.84 | 32.78 |
| | MPROX: Mean proximity index | 9948.18 | 42,631.88 | 107,968.34 |
| Diversity metrics | CR: Class richness | 5 | 5 | 5 |
| | SHDI: Shannon’s diversity index | 1.270 | 1.245 | 1.043 |
| | SHEI: Shannon’s evenness index | 0.789 | 0.773 | 0.648 |

**Table 2.8.** Area and edge metrics at the class level, for 1947, 1979, and 2019.

| Metric | Class | 1947 | 1979 | 2019 |
|---|---|---|---|---|
| CA: Total class area (ha) | ABE | 1280.83 | 1888.41 | 2597.82 |
| | TRS | 988.49 | 1034.21 | 923.29 |
| | HER | 1653.23 | 1004.87 | 427.03 |
| | SPV | 71.84 | 76.50 | 54.89 |
| | AQU | 166.35 | 156.75 | 157.71 |
| CP: Class proportion (%) | ABE | 30.78 | 45.39 | 62.44 |
| | TRS | 23.76 | 24.86 | 22.19 |
| | HER | 39.73 | 24.15 | 10.26 |
| | SPV | 1.73 | 1.84 | 1.32 |
| | AQU | 4.00 | 3.77 | 3.79 |
| LPI: Largest patch index (%) | ABE | 29.02 | 43.33 | 60.45 |
| | TRS | 0.66 | 1.03 | 0.93 |
| | HER | 2.82 | 1.43 | 0.22 |
| | SPV | 0.45 | 0.49 | 0.92 |
| | AQU | 3.16 | 2.22 | 2.10 |
| MPS: Mean patch size (ha) | ABE | 10.41 | 15.74 | 21.65 |
| | TRS | 1.32 | 1.31 | 1.18 |
| | HER | 4.08 | 1.82 | 0.70 |
| | SPV | 1.36 | 1.42 | 1.83 |
| | AQU | 33.27 | 31.35 | 9.86 |
| MPE: Mean patch edge (m) | ABE | 6015.93 | 8559.07 | 9474.38 |
| | TRS | 863.69 | 1111.26 | 1223.57 |
| | HER | 1264.95 | 923.00 | 665.25 |
| | SPV | 767.90 | 801.37 | 830.30 |
| | AQU | 6570.87 | 6441.96 | 2341.89 |
| ED: Edge density (m/ha) | ABE | 577.72 | 543.89 | 437.65 |
| | TRS | 655.31 | 846.71 | 1037.65 |
| | HER | 309.88 | 507.94 | 944.06 |
| | SPV | 566.52 | 565.67 | 453.80 |
| | AQU | 197.50 | 205.49 | 237.59 |

**Table 2.9.** Shape metrics at the class level, for 1947, 1979, and 2019.

| Metric | Class | 1947 | 1979 | 2019 |
|---|---|---|---|---|
| MPAR: Mean perimeter-area ratio | ABE | 0.185 | 0.153 | 0.168 |
| | TRS | 0.101 | 0.130 | 0.153 |
| | HER | 0.079 | 0.102 | 0.125 |
| | SPV | 0.096 | 0.109 | 0.098 |
| | AQU | 0.126 | 0.046 | 0.066 |
| MSI: Mean shape index | ABE | 2.817 | 2.965 | 2.909 |
| | TRS | 2.263 | 2.829 | 3.259 |
| | HER | 2.010 | 2.235 | 2.361 |
| | SPV | 2.055 | 2.222 | 1.915 |
| | AQU | 3.760 | 3.247 | 2.071 |
| MFD: Mean fractal dimension | ABE | 1.518 | 1.512 | 1.521 |
| | TRS | 1.461 | 1.513 | 1.546 |
| | HER | 1.414 | 1.453 | 1.489 |
| | SPV | 1.439 | 1.459 | 1.436 |
| | AQU | 1.501 | 1.416 | 1.389 |

**Table 2.10.** Aggregation metrics at the class level, for 1947, 1979, and 2019.

| Metric | Class | 1947 | 1979 | 2019 |
|---|---|---|---|---|
| NP: Number of patches | ABE | 123 | 120 | 120 |
| | TRS | 750 | 788 | 783 |
| | HER | 405 | 553 | 606 |
| | SPV | 53 | 54 | 30 |
| | AQU | 5 | 5 | 16 |
| MENND: Mean Euclidean nearest neighbour distance (m) | ABE | 29.51 | 20.73 | 6.71 |
| | TRS | 18.73 | 17.36 | 17.63 |
| | HER | 21.30 | 27.47 | 30.72 |
| | SPV | 126.96 | 247.82 | 408.95 |
| | AQU | 181.13 | 123.33 | 342.81 |
| MPROX: Mean proximity index (for a 100 m buffer) | ABE | 87,302.27 | 526,604.25 | 1,389,437.08 |
| | TRS | 647.79 | 1340.99 | 1299.65 |
| | HER | 5036.90 | 964.48 | 201.06 |
| | SPV | 161.31 | 69.81 | 187.65 |
| | AQU | 3650.34 | 2822.40 | 826.43 |
| DIV: Division index | ABE | 11.10 | 8.85 | 6.24 |
| | TRS | 99.37 | 99.19 | 99.23 |
| | HER | 97.95 | 98.64 | 99.59 |
| | SPV | 89.01 | 88.26 | 50.54 |
| | AQU | 35.13 | 59.05 | 64.32 |

# Chapter 3.

# Assessment of land cover trajectories as an indicator of urban habitat temporal continuity

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## 3.1. Abstract

The trends of land cover dynamics in cities have major repercussions on urban biodiversity, ultimately impacting the health and well-being of human urbanites. Older habitats, i.e., habitats with higher spatiotemporal continuity, allow ecosystem processes promoting the maintenance of diverse microhabitats and the accommodation of diverse species over time, contributing for a richer biodiversity at the city level and beyond. Thus, we implement the analysis of land cover trajectories proposed as an indicator of habitat continuity, in order to identify priority areas for conservation or restoration that can be integrated in urban planning. The method was applied in the city of Porto, Portugal, and it was used to detect the main habitat patches associated with trends of vegetation persistence, gain and loss, between 1947 and 2019. The most common change was related to urbanisation processes, where artificial built elements replaced areas of tree, shrub and herbaceous cover, completely dominating the territory in 2019 (66% cover). Moreover, tree and shrub cover had a relatively balanced dynamics, keeping a constant area (20-25%) while newly created wooded habitats compensated for the lost ones. Finally, areas covered with herbaceous vegetation suffered a drastic loss and fragmentation over the period of 72 years (from 40% in 1947 to 10% in 2019). This analysis of land cover evolution allowed for the identification of areas that have been continuously covered by vegetation, displaying a greater stability and higher probability of habitat continuity. This information, with its spatially explicit character, can help to inform future planning, design and management policies at a local scale and contribute to the conservation, restoration and expansion of urban habitats and their biodiversity.

**Keywords**: habitat conservation; land cover change; local scale; spatial prioritization; urban biodiversity; urban planning.

## 3.2. Introduction

Habitat loss and transformation is one of the major threats to biodiversity and urbanisation is one of the main culprits (McKinney, 2002; Simkin et al., 2022; Tilman et al., 2017). Human populations are frequently settled in areas with rich soils and vegetation, often near waterbodies, which can exhibit high levels of biodiversity (Chapman & Underwood, 2009; Ives et al., 2016; Kowarik, 2011). However, urbanisation

causes the destruction, degradation, fragmentation and isolation of natural habitats, alteration of natural disturbance regimes and introduction of non-native species (Gaertner et al., 2017; Kowarik, 2011). On the other hand, urbanisation is responsible for the emergence of new habitats in these areas, creating a diverse mosaic of semi-natural and man-made habitats, home to unique assemblies of flora and fauna species (Müller et al., 2013; Spotswood et al., 2021).

Urban biodiversity is crucial for ecosystem functioning (Harrison et al., 2014; Millennium Ecosystem Assessment, 2005; Pedersen Zari, 2018) and it is beneficial to the health, well-being, and quality of life of urban residents (Aerts et al., 2018; Schebella et al., 2019). Preservation and promotion of urban biodiversity is fundamental if cities want to tackle climate challenges and achieve sustainability (C.-W. Huang et al., 2018; Xie & Bulkeley, 2020). As such, it is thus essential that urban planning and landscape design integrate actionable ecological knowledge (Garrard et al., 2018; Zhou et al., 2019), ideally including spatially explicit data and at the appropriate spatial and temporal scales (Aronson et al., 2017; Borgström et al., 2006; Jarvis & Young, 2005; Opdam et al., 2013). With urban biodiversity conservation in mind, planners and decision makers must plan for the availability of relevant habitats, specific to each geographic context. In addition to the creation of new urban green spaces, it is imperative to preserve the oldest habitats (Kowarik & von der Lippe, 2018; McKinney, 2002). While newly created habitats can show high species richness, they are commonly occupied by non-native species and generalist native species that can tolerate a diverse range of conditions and disturbance (Callaghan et al., 2019; Ducatez et al., 2018). If habitat quality is maintained, habitat continuity (i.e. the persistence of a particular habitat type through time) supports the occurrence of specialist species in these old habitats (Lõhmus & Liira, 2013; Nordén et al., 2014; Raduła et al., 2020) and consequently promotes a higher species diversity at the city level.

However, despite the call for action of international experts and institutions (e.g. ICLEI, 2020; Secretariat of the Convention on Biological Diversity, 2012), many cities face multiple challenges to manage and preserve their biodiversity (Cooper et al., 2021; Wilkinson et al., 2013). In this context, there is still a lack of ecological knowledge on the functioning of the urban ecosystem and, frequently, the available data is inadequate to meet the requirements of urban planners, designers and managers (Jarvis & Young, 2005; Zhou et al., 2019), especially at the local level (McDonnell & Hahs, 2013; Wilkinson et al., 2013). Remarkably, this is the level where planning and management decisions directly translate into site interventions that modify urban habitats (Brown, 2017; Opdam

et al., 2013). There is often a disconnection between the spatial and temporal scale of ecological information and the practices and policies that influence the urban environment (Borgström et al., 2006; Opdam et al., 2013; Uchida et al., 2021), which makes it difficult to integrate scientific data in spatial planning and urban habitat conservation programs (Brown, 2017; Łopucki & Kiersztyn, 2015; Opdam et al., 2013). Spatialization of ecological data is considered a fundamental tool to improve the communication between multidisciplinary scientific teams and non-expert decision-makers and to contribute to generate knowledge that is useful to inform urban planning, design and management (Jarvis & Young, 2005; Pedersen et al., 2004).

Habitat availability (in space and time) is an important determinant of species dynamics and several authors have highlighted the importance of its temporal aspect (M. L. Cadenasso et al., 2006; Hanski, 1999), particularly in urban ecosystems (Alberti et al., 2020; Müller et al., 2013; Ramalho & Hobbs, 2012). However, it is most common that in urban ecology studies, habitat availability is evaluated from a merely static perspective, which disregards the intrinsic dynamism of urban environments. Few urban ecological studies include the temporal component (Ossola, Cadenasso, et al., 2021); this can be assessed as patch continuity, habitat age, site history, or land-use legacy (e.g. Gustavsson et al., 2007; Johnson et al., 2018). The temporal aspect of habitat availability can influence the occurrence of diverse organisms over time through a multitude of processes. For example, it interferes with processes typically associated with metapopulation or metacommunity dynamics, such as dispersal, (re)colonization, and extinction, by causing time-lagged responses to landscape change, which in turn can cause a phenomenon of extinction debt or immigration (or species) credit (Lira et al., 2019; Swan et al., 2021; Uroy et al., 2021). Furthermore, habitats with higher continuity, i.e., those older and more stable, offer better conditions for specialist species, as these are often associated with habitat niches that take time to develop, such as tree cavities or wood decay (Janssen et al., 2017; Nordén et al., 2014).

In the scope of biodiversity conservation in an urban context, the following questions arise: Which, and where, are the areas that present a higher probability of habitat continuity in time? How can they be rapidly identified in a context of insufficient biodiversity data and low financial resources? In this regard, here we propose the analysis of land cover trajectories as an indicator of habitat continuity, in order to identify priority areas for conservation or restoration that can be integrated in urban planning. Using the city of Porto, in Portugal, as a case study, our research objectives were: 1) to determine and spatially represent the land cover trajectories from the mid-20$^{th}$ century to

a recent date; 2) to assess the main changes in vegetation patches in terms of persistence, gain or loss; 3) to identify the habitat patches subject to a lesser degree of habitat disruption and, consequently, exhibiting a higher degree of continuity.

## 3.3. Methods

### *3.3.1. Study area*

This study focuses on the Municipality of Porto, located in the northern region of Portugal (Figure 3.1). Porto presents itself as a relatively small city (42 km$^2$, 232,000 inhabitants; INE, 2022), but it is the centre of a dynamic metropolitan area comprised of 17 municipalities and around 1.7 million residents (AMP, 2022). Its privileged location at the intersection of the Douro River and the Atlantic Ocean and the mild temperate climate (*Csb* regime, Koppen-Geiger classification; Peel et al., 2007) conduced to a rich human history, as well as rich biodiversity levels (Guilherme et al., 2015).

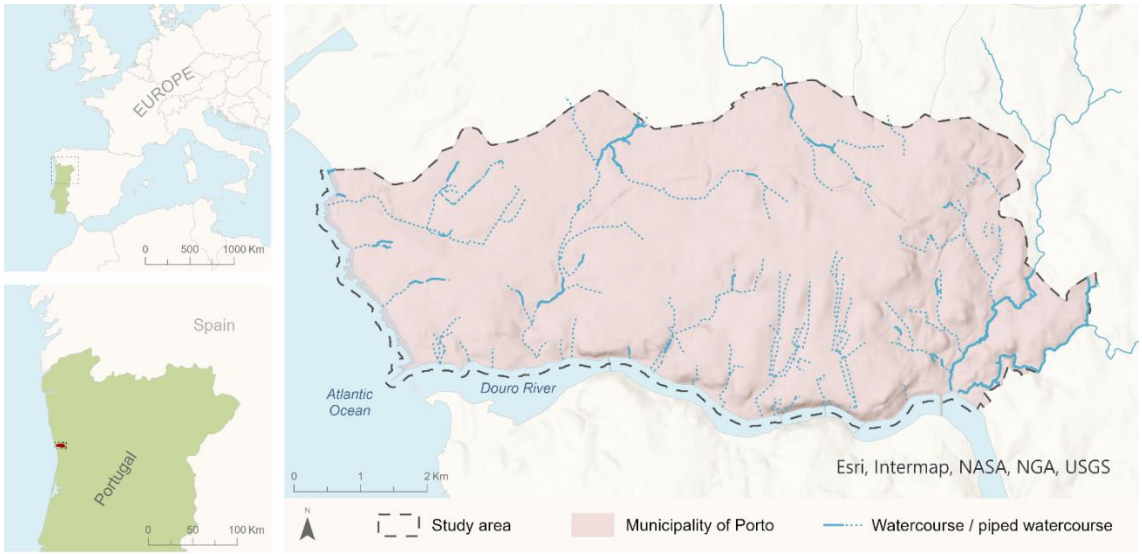



**Figure 3.1.** Location of the study area, in northern Portugal.

### *3.3.2. Land cover trajectories*

This study follows the work of Guilherme et al. (2022), which classified the land cover in Porto for the years 1947, 1979 and 2019, based on aerial photography and satellite

imagery, using an adaptation of the UrHBA method (Farinha-Marques et al., 2017). UrHBA methodology is spatially explicit, based on the visual interpretation of the landscape and it excels at capturing urban habitat diversity at a fine scale. The mapping and classification of land cover was made in vectorial format in a GIS environment, with the older images being previously orthorectified (Guilherme et al., 2022). In a context of limited time and resources, and due to the limitations of historic remote sensing data, the mapping procedure was streamlined – all elements were mapped as patches, even if with a linear shape; the minimum dimension for patches to be distinguished was 2000 $m^2$, and the minimum width was 5 m. The classification was also simplified to five land cover categories: 1) Artificial Built Elements, ABE, 2) Trees and Shrubs, TRS, 3) Herbaceous, HER, 4) Sparsely Vegetated - Terrestrial, SPV, and 5) Sparsely Vegetated - Aquatic, AQU (see Guilherme et al., 2022 for more details). In an urban context, ABE consists of impervious surfaces and buildings; TRS identifies all tree and shrub cover, which can occur in parks, gardens, forested areas, scrub/bushland, riparian galleries, wooded crops, tree-lined streets, etc.; HER marks all areas covered by herbaceous vegetation, including both areas only temporarily covered with herbaceous vegetation and areas with frequent arrest to successional processes to maintain a permanent herbaceous cover, such as lawns, meadows, allotment or vegetable gardens, herbaceous crops, pastures, semi-natural grasslands, spontaneous vegetation in vacant lots, etc.; SPV consists of every type of non-vegetated soil, such as bare soil, sand, and rock; AQU comprises water surfaces, such as the sea, rivers, lakes, and ponds (including artificial water elements).

The method is based on the concept of land cover, which refers to the physical material that covers the surface of the land (R. Haines-Young, 2009; Jarvis & Young, 2005) and is easily applicable in a multitude of geographic contexts as it transcends local and cultural conditions (Farinha-Marques et al., 2017). It seems particularly relevant in urban ecological studies as it is associated with habitat types (Farinha-Marques et al., 2017) and it can be directly transformed through most urban interventions, not necessarily requiring a change in land use type (R. Haines-Young, 2009). At a fine scale, land use classification, being strongly associated with socio-economic activities, could fail to capture small habitat patches as the vegetation categories can occur in a variety of land use types; likewise, areas classified with the same land use type could encompass different vegetation covers.

Land cover trajectories are a common method to assess trends of landscape change over time, usually derived from satellite images or aerial photograph, at a particular

location and at multiple dates (Gbanie et al., 2018; D. Liu & Cai, 2012). As such, the land cover layers for 1947, 1979 and 2019 (in vectorial format; Guilherme et al., 2022) were overlapped, using the "intersect" tool in ArcMap Desktop 10.5. This generated a new layer of information regarding the trajectory of land cover for the entire surface of the city. To reduce errors and/or biases and to simplify the data analysis, this process included the elimination of sliver polygons (smaller than 100m$^2$), i.e., they were absorbed into larger adjoining polygons; this was achieved with the "eliminate" tool (ArcMap Desktop 10.5). In the newly created layer, each polygon is then described by a sequence of three land cover categories, i.e., a land cover trajectory, reflecting its evolution from 1947, to 1979 and to 2019, as illustrated in Figure 3.2. The resulting data allowed for the analysis of the transition in land cover considering three different time intervals: 1) from 1947 to 1979; 2) from 1979 to 2019; and 3) the complete sequence from 1947, to 1979, then to 2019.

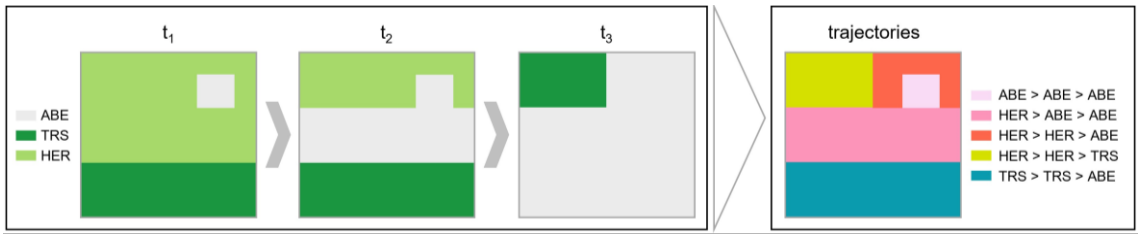



**Figure 3.2.** Demonstrative example of the method for the classification of trajectories, using UrHBA categories in vectorial format.

### *3.3.3. Changes in vegetation cover*

Focusing particularly on vegetated areas, we analysed in more detail the land cover transformations that occurred in the study area, for trajectories related to TRS cover, HER cover and general vegetation cover (combining both TRS and HER in the same analysis). The areas were classified according to the chronological occurrence of vegetation as follows: 1) persistent cover - present in 1947, 1979 and 2019; 2) gained cover - absent in 1947, but present in 2019; 3) disturbed cover - present in 1947 and 2019, but absent in 1979; 4) gained then lost cover - absent in 1947 and 2019, but present in 1979; 5) lost cover - present in 1947 and absent in 2019.

The analysis of vegetation evolution led to the identification of the areas with persistent vegetation cover, i.e., areas that were covered with vegetation in 1947, 1979, and 2019.

The areas with persistent vegetation were considered to have a higher probability of habitat continuity and, consequently, the areas with the most concentration of persistent vegetation were identified as the most important for habitat conservation and regeneration. Besides habitat continuity, these areas were also prioritized based on vulnerability to future land cover change, which was assessed based on their framing within urban planning instruments (Câmara Municipal do Porto, 2021a, 2021b), current land use, ownership, and accessibility. On one extreme, the areas with persistent vegetation that are included in environmental plans, that are currently integrated in green spaces, on the public domain, and publicly accessible, are considered the least vulnerable (and thus, the least priority). On the other extreme, the areas located in zones intended for urban development, that have no current use, are private domain, and are not publicly accessible, are considered the most vulnerable to habitat destruction and we consider they should be the top priority for conservation. For this purpose, vegetation patches located in public parks and gardens were considered to be the least susceptible to habitat destruction, as these areas tend to be preserved on the long term, since their conservation is usually included in urban plans and policies. Vegetation patches integrated on the green spaces of public and private services facilities (such as schools and hospitals) were classified as moderately susceptible, as these are relatively valued but are more prone to destruction when compared to public parks and gardens, as they are not included in environmental plans and policies. On the other hand, vegetation mainly located in undeveloped land or private green spaces was considered the most vulnerable to habitat loss, as these areas are frequently subject to urban pressure, being classified as areas destined to urban development.

## 3.4. Results

### *3.4.1. Land cover trajectories*

The study of the dynamics of land cover transformation in Porto revealed 106 trajectories, amongst 125 possible ones, considering the set of five land cover categories. Of these trajectories, 11 stood out as predominant, covering in total more than 80% of the territory (Figure 3.3). As an overall trend, derived by urbanisation, over 62% of the study area has retained or acquired a higher degree of artificialization, i.e., marked by the coverage of Artificial Built Elements (ABE). Nevertheless, a considerable proportion of land has also maintained a less artificial land cover, namely Trees and Shrubs (TRS) and Herbaceous (HER), throughout the analysed period of 72 years.

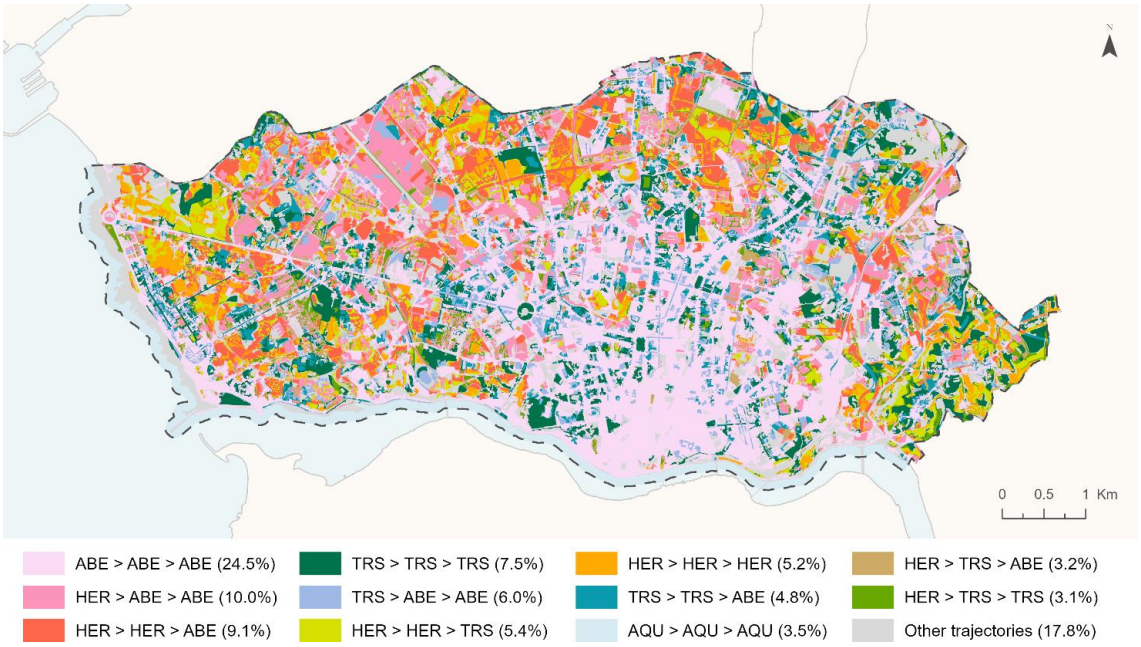



**Figure 3.3.** Land cover trajectories from 1947, to 1979 and to 2019 (1947 > 1979 > 2019). Land cover categories: ABE, Artificial Built Elements; TRS, Trees and Shrubs; HER, Herbaceous; SPV, Sparsely Vegetated Terrestrial; AQU, Sparsely Vegetated Aquatic.

**Table 3.1.** Different situations of land cover dynamics and variation (and its distribution throughout the city).

| Land cover dynamics | Area (ha) | Proportion (%) | Land cover variation | Area (ha) | Proportion (%) |
|---|---|---|---|---|---|
| Land cover never changed | 1722.40 | 41.4% | Same land cover in 1947, 1979, and 2019 | 1722.40 | 41.4% |
| Land cover changed once | 1853.44 | 44.6% | Same land cover in 1947 and 1979 | 956.21 | 23.0% |
| | | | Same land cover in 1979 and 2019 | 897.23 | 21.6% |
| Land cover changed twice | 585.91 | 14.0% | Same land cover in 1947 and 2019 | 267.07 | 6.4% |
| | | | Different land cover in 1947, 1979, and 2019 | 318.84 | 7.6% |

The city of Porto revealed a relatively dynamic land cover evolution, where almost 60% of the territory has experienced at least one change in its land cover since 1947 (Table 3.1). A smaller portion has been through multiple transformations, with 7.6% of the study area exhibiting three different land cover for the three analysed moments.

The city of Porto has experienced a marked increase in urbanisation since the mid-20th century. From 1947 to 1979, the area covered by Artificial Built Elements (ABE) has increased by 47.7% (while maintaining 85.4% of their previous patches; Figure 3.4); this growth was supported by the replacement of areas previously covered by herbaceous vegetation (HER, 494.60 ha), but also by trees and shrubs (TRS, 286.18 ha; Figure 3.4; Table 3.2). From 1979 to 2019, the increment in ABE is also notorious; this time, ABE cover has incremented by 37.66%, while retaining almost 90% of previous areas. The destruction of vegetation patches continues to be the main source of land cover change, with 420.03 ha of TRS cover and 462.96 ha of HER cover being replaced by ABE cover (Figure 3.4; Table 3.2). Artificial Built Elements (ABE) is the least dynamic category (besides AQU), since it retains almost all of the previous cover, experiencing mainly irreversible gains throughout the years (Figure 3.4; Table 3.2). The most significant exception is the change from ABE to TRS (both from 1947 to 1979 and from 1979 to 2019), which is generally related to the implementation and growth of tree cover in streets and squares, in residential areas and in previously industrial areas (following the demolition of factory buildings).

The area covered by TRS cover has remained relatively constant for the analysed period. However, vegetation patches with this cover experienced a fair number of changes (Figure 3.4, Table 3.2). In fact, only approximately half of the TRS cover was maintained in each of the transitions (from 1947 to 1979 and from 1979 to 2019), while the rest was transformed mainly to ABE, but also HER cover.

As also seen in Table 3.2 and Figure 3.4, for both time intervals, areas of HER cover have also been gradually substituted, in considerable proportions, by areas of TRS cover (309.84 ha for 1947-1979, 282.13 ha for 1979-2019). The category of HER cover went from being the predominant class, in 1947 (40% cover), to one of the least abundant land cover categories (10% cover), being surpassed by both ABE and TRS.

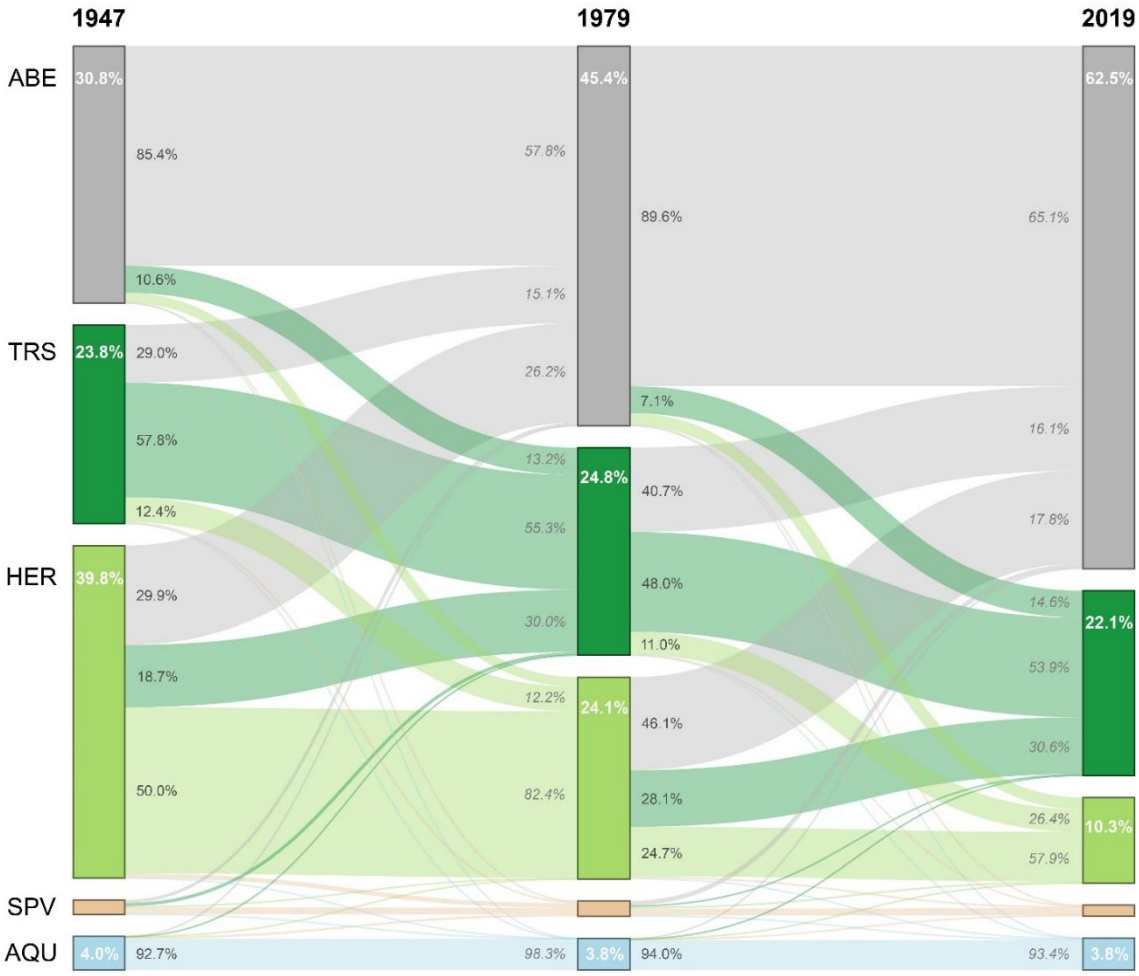



**Figure 3.4.** Diagrammatic representation of the evolution of land cover in Porto, from 1947, to 1979 and to 2019 (created with "SankeyMATIC", at www.sankeymatic.com). Land cover categories: ABE, Artificial Built Elements; TRS, Trees and Shrubs; HER, Herbaceous; SPV, Sparsely Vegetated Terrestrial; AQU, Sparsely Vegetated Aquatic. White values refer to the proportions of each land cover category for each of the three years; dark values indicate: 1) the proportion of the original land cover that followed that path (regular text on the right side of the bars), 2) the proportion of the target land cover that followed that path (italicized text on the left side of the bars); only the values that relate to transformations that occurred in over 100ha appear in the figure.

The categories of Sparsely Vegetated – Terrestrial (SPV) and Sparsely Vegetated – Aquatic (AQU) are strongly associated with the coastal and river lines (beaches, cliffs, sea, and watercourses), that have remained relatively stable at the city level (Figure 3.4; Table 3.2). However, it should be noted that a relatively large surface of SPV cover has been replaced by ABE, especially in the period 1979-2019. The changes seen in the category of SPV are related to tidal variation, construction in previously vacant lots, abandonment of sediment extraction sites and regeneration of previously deforested sites, whereas for AQU it mainly reflects tidal variation, the artificialization of coastal and riverfront and the built-up of bridges. For the remainder of this article, SPV and AQU evolution will not be discussed further, as it is outside the main scope of this research.

**Table 3.2.** Land cover conversion matrix from 1947 to 1979 and from 1979 to 2019 (area, ha).

| Land cover | | 1979 | | | | | Total (1947) | Change |
|---|---|---|---|---|---|---|---|---|
| | | ABE | TRS | HER | SPV | AQU | | |
| 1947 | ABE | 1092.96 | 135.89 | 48.07 | 2.53 | 0.41 | 1279.86 | + 47.7% |
| | TRS | 286.18 | 570.99 | 122.13 | 9.01 | 0.19 | 988.50 | + 4.5% |
| | HER | 494.60 | 309.88 | 827.07 | 22.36 | 0.33 | 1654.24 | - 39.3% |
| | SPV | 14.81 | 16.02 | 5.90 | 33.44 | 1.68 | 71.85 | + 7.8% |
| | AQU | 1.55 | 0.29 | 0.22 | 10.08 | 154.15 | 166.29 | - 5.7% |
| **Total (1979)** | | 1890.10 | 1033.07 | 1003.39 | 77.42 | 156.76 | 4160.74 | |
| Land cover | | 2019 | | | | | Total (1979) | Change |
| | | ABE | TRS | HER | SPV | AQU | | |
| 1979 | ABE | 1693.55 | 134.20 | 58.70 | 2.77 | 0.88 | 1890.10 | + 37.7% |
| | TRS | 420.03 | 496.09 | 113.27 | 3.19 | 0.49 | 1033.07 | - 10.9% |
| | HER | 462.84 | 281.71 | 247.79 | 6.39 | 4.66 | 1003.39 | - 57.3% |
| | SPV | 22.02 | 7.74 | 8.42 | 34.90 | 4.34 | 77.42 | - 32.3% |
| | AQU | 3.79 | 0.45 | 0.09 | 5.14 | 147.29 | 156.77 | + 0.6% |
| **Total (2019)** | | 2602.23 | 920.19 | 428.27 | 52.38 | 157.67 | 4160.74 | |

### *3.4.2. Changes in vegetation cover*

Now focusing on vegetation patches, the results revealed substantially different patterns of land cover transformation for TRS and HER categories. Regarding arboreal vegetation (Figure 3.5.a), over 40% of the study area was covered by TRS at some point between 1947 and 2019. While a considerable proportion of the territory faced the loss of TRS cover (14.3% of the study area), this was somehow compensated by the gain in TRS cover in other areas (12.7% of the study area).

A significant portion of the city (7.5%) has been permanently covered by TRS since 1947, mainly organized in large patches (Figure 3.5.a). To a similar extent, some areas (6.7% of the study area) experienced a gain of TRS cover between 1947 and 1979 but were later occupied by artificial elements between 1979 and 2019.

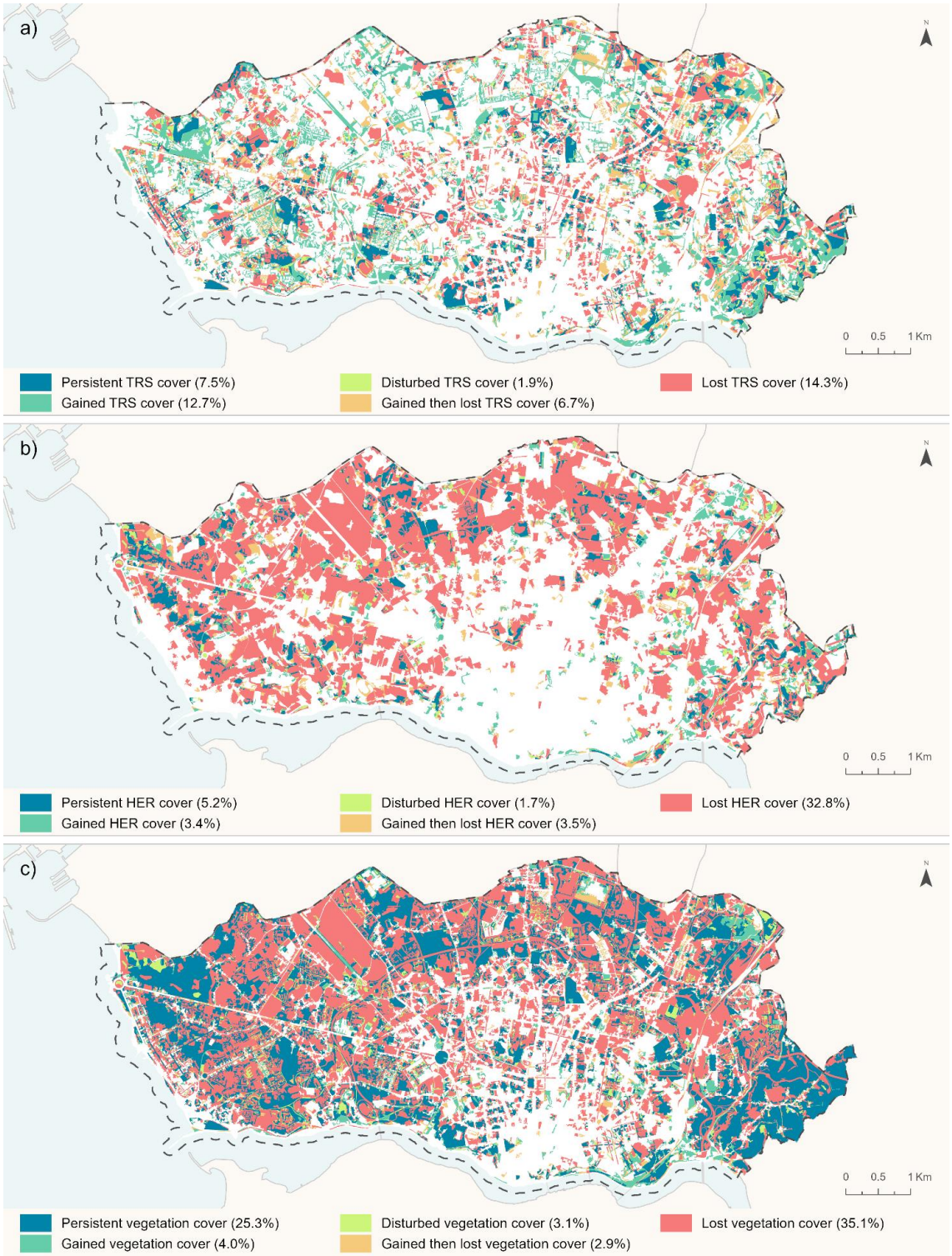



**Figure 3.5.** Patterns of land cover change involving: a) TRS, Trees and Shrubs, b) HER, Herbaceous, and c) overall vegetation.

In contrast with the more balanced changes in tree cover, the evolution of herbaceous vegetation identifies a clear dominant trend towards the loss of the majority of patches of HER cover category (Figure 3.5.b). While almost half of the city was covered with herbaceous vegetation at some point between 1947 and 2019, the loss of HER cover occurred in about a third of the study area (32.8%) for the same period. In about 10% of the territory, HER cover was replaced by TRS. However, the most common change was from HER to ABE (in over 20% of the study area). On the contrary, only 5.2% of the city area corresponds to persistent herbaceous patches, from 1947 to 2019. Some new herbaceous patches were created in the analysed period, but the gain of HER cover is not expressive at the city scale.

Considering all vegetated areas (Figure 3.5.c), whether covered by herbaceous or wooded vegetation, it becomes clear that some large areas have been spared from construction since, at least, 1947, and they are mainly concentrated in the western, eastern, and northern sections of the city (amounting to 25.3% of the study area). On the other hand, more than one third of the territory (35.1%) has experienced the complete loss of vegetation cover; this trend is very noticeable in the periphery of the city, due to the urban sprawl of the second half of the 20$^{th}$ century (Figure 3.5.c). In this overall analysis, the areas that gained vegetation cover were almost negligible.

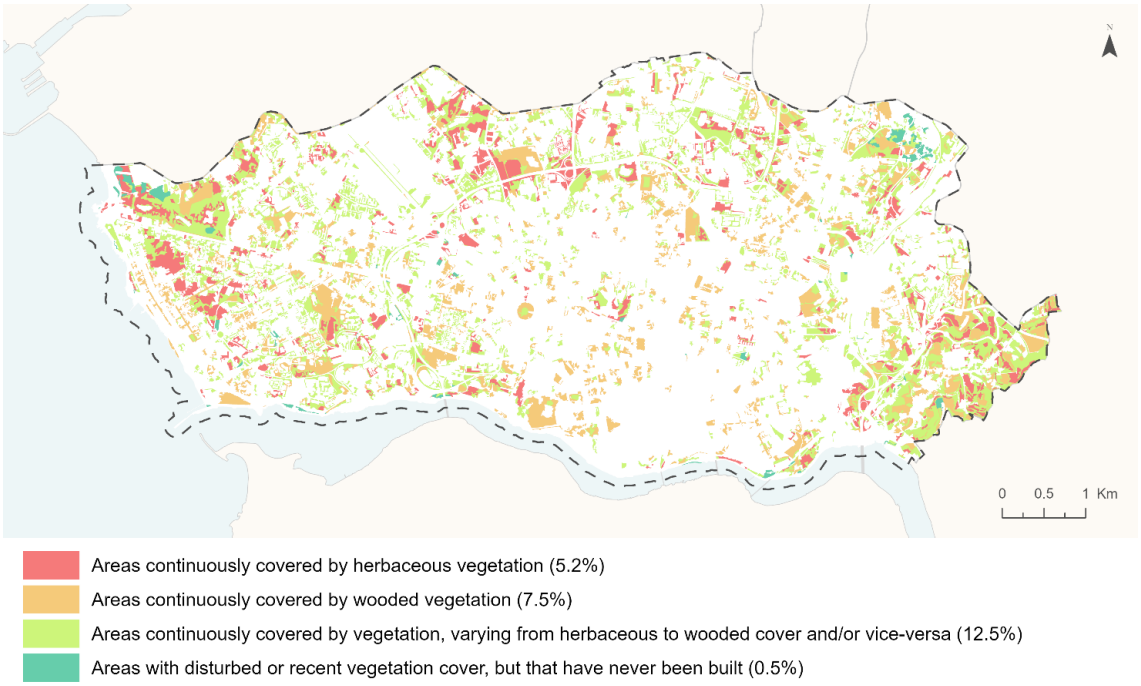



**Figure 3.6.** Vegetated areas with higher stability and higher probability of habitat continuity.

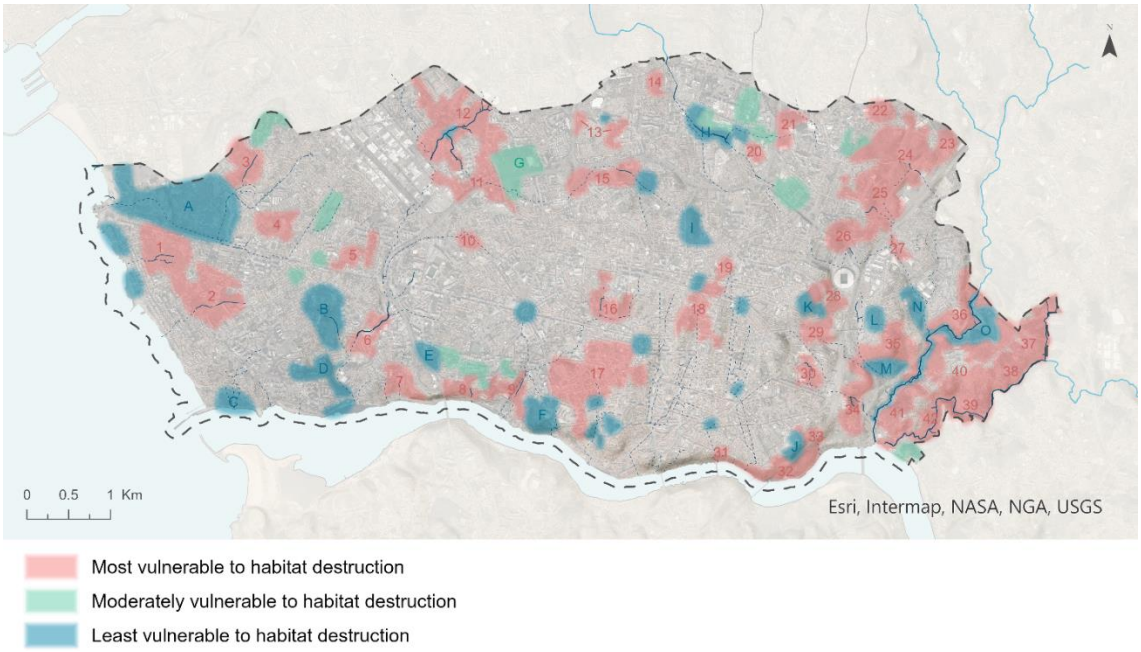



**Figure 3.7.** Main sections of the city with higher habitat continuity, graded by their vulnerability to habitat destruction; for a complete legend see Table 3.3 (source of background imagery: Direção-Geral do Território, 2018).

**Table 3.3.** List of the main priority areas for the conservation of habitats with higher continuity (see Figure 3.7).

| | | |
|---|---|---|
| **Areas comprising mainly parks and gardens:** | | |
| A. City Park | F. Crystal Palace Garden | K. São Roque Park |
| B. Serralves Park | G. Prelada Park | L. Corujeira Garden |
| C. Passeio Alegre Garden | H. Asprela Park | M. Quinta da Bonjóia |
| D. Pasteleira Park | I. Covelo Park | N. future Alameda de Cartes Park |
| E. Botanical Garden | J. Nova Sintra Park | O. Oriental Park |
| **Areas comprising mainly undeveloped land and/or private property:** | | |
| 1. Ribeira de Nevogilde | 15. Regado | 29. 25 de Abril |
| 2. Ribeira da Ervilheira | 16. Burgães / Lapa | 30. Godim |
| 3. Ribeira de Aldoar | 17. Cedofeita | 31. Fontainhas |
| 4. Mata de Aldoar | 18. Santa Catarina | 32. Quinta da China |
| 5. Pinheiro Manso | 19. Lima | 33. Formiga |
| 6. Lordelo | 20. Lamas | 34. Pinheiro de Campanhã |
| 7. Ribeira do Ouro | 21. Areosa Ocidental | 35. Corujeira / Monte da Bela |
| 8. Via Panorâmica | 22. Areosa Oriental | 36. Tirares / Pego Negro |
| 9. Ribeira de Vilar / Pena | 23. Ranha | 37. Areias |
| 10. Francos | 24. Currais | 38. Furamontes |
| 11. Prelada | 25. Contumil | 39. Granja |
| 12. Viso / Requesende | 26. Salgueiros | 40. Azevedo |
| 13. Telheira | 27. São Roque da Lameira | 41. Quinta da Revolta |
| 14. Azenha | 28. Lameira de Cima | 42. Rio Torto |

This analysis of land cover trajectories allowed to detect which areas have been continuously covered by vegetation, displaying a higher stability and higher probability of habitat continuity. As highlighted in Figure 3.6, around 25% of the territory has been consistently covered by vegetation, but approximately half of this area experienced significant habitat changes, transitioning from wooded to herbaceous vegetation or vice-versa. Patches of relatively stable habitat are restricted to 12.7% of the city surface and include wooded and herbaceous habitats in similar proportions. Habitats with continuous tree and shrub cover are scattered throughout the entire study area, while the habitats with continuous herbaceous cover are concentrated in the western, eastern, and northern sections.

This research allowed for the identification of the main sections of the city that have a greater conservation value based on the criteria of habitat temporal continuity, while also considering their susceptibility to habitat loss, based on their protection status in urban planning programs, current land cover, ownership, and accessibility (Figure 3.7; Table 3.3). This spatially explicit representation can be particularly useful for communication and knowledge dissemination. Indeed, while the areas with high probability of habitat continuity are evenly distributed throughout the city, the eastern and northern sections face a lack of protection of these important green spaces. The majority of the older vegetation patches in the northern and eastern section is located in private undeveloped land, unlike the most western section, where they are generally integrated in parks and gardens.

## 3.5. Discussion

The global trend of increasing urbanisation and loss of vegetated areas (Güneralp et al., 2020; Radwan et al., 2021; Richards & Belcher, 2020) was also experienced in Porto. This phenomenon of declining vegetation cover being associated with urban expansion and densification has been reported by numerous authors in cities and metropolitan areas around the world (e.g. Lennert et al., 2020; Zaitunah et al., 2021; Zubair, 2021). Some authors have also investigated the relation between urban expansion and vegetated areas for the particular case of Porto. For example, Madureira et al. (2011) analysed the evolution of the green structure in Porto and highlighted its severe decline and fragmentation throughout the 20$^{th}$ century, especially for agricultural areas. In a comparison between multiple cities, Bagan and Yamagata (2014) noticed a similar

pattern for Porto, where the increase in urban area resulted in the destruction of forest, cropland and grassland.

Nevertheless, except for a few cases, the research on urban site history or urban land cover trajectories is still very incipient, especially at the local level. The local landscape level is defined by Opdam et al. (2013) as the "areas where physical landscapes interact directly with social networks of land owners, managers, and landscape users". This is particularly relevant in urban landscapes, where the ecological dynamics are constantly affected by local scale decisions such as the planning, design and management of individual sites and infrastructures (Brown, 2017; Kremer et al., 2016). The study of land cover trajectories of Porto unravelled the history of each site and allowed to infer the temporal continuity of each vegetation patch, which was achieved at a very fine scale for the entire city. Past land use and land cover have an impact on ecosystem functioning, as they influence current landscape conditions and affect future responses to environmental change (Foster et al., 2003; Ramalho & Hobbs, 2012). The current assemblies of urban biodiversity are a result of the interaction between landscape heterogeneity and connectivity, which are influenced by the age and history of each site or habitat patch (Alberti et al., 2020; Alberti & Wang, 2022; M. L. Cadenasso et al., 2006; Foster et al., 2003). Older habitats, i.e. those that are more stable and that underwent the least transformation, are considered to harbour higher biodiversity levels (Janssen et al., 2017; Nordén et al., 2014; Raduła et al., 2020). For this reason, habitat age or temporal continuity can be used as a valuation criteria for the conservation of urban habitats (Jarvis & Young, 2005; Wittig & Schreiber, 1983).

The analysis of land cover change in Porto showed a highly dynamic urban landscape. Only around 40% of the study area has remained relatively stable in terms of land cover during the study period; this value seems to be a bit lower than the average reported for other southern European cities (e.g. Frondoni et al., 2011) and it mostly regards land that was already urbanised in the mid-20$^{th}$ century. The most noticeable land cover transformation in Porto is related to urbanisation processes that drastically reduced and fragmented vegetation patches, which is comparable to other urban areas (Tello et al., 2020; Zaitunah et al., 2021).

Tree and shrub (TRS) cover revealed a dynamic history in Porto since 1947, despite maintaining a constant proportion in the city throughout the years – a fair portion of the old TRS patches were destroyed (597 ha or 14.3% of the study area), but others were created elsewhere in a similar extent (529 ha or 12.7%). Large patches of forestry and wooded crops were gradually replaced by urbanisation (ABE), especially in the

periphery. It is also noteworthy the loss of TRS cover in smaller spaces, spread throughout the centre and in the western extremity (the oldest parts of the city), which once formed a network of tree-covered private gardens and tree-lined streets which was lost over time. The areas that experienced a gain in TRS cover reflect two main trends, both of which occurred mainly in patches previously dominated by herbaceous vegetation: 1) the abandonment of former agricultural fields, where the natural course of ecological succession originated wooded habitat patches; 2) the construction of residential buildings surrounded by wooded green spaces. Around 314 ha (or 7.5% of the study area) consists of land continuously covered by trees and shrubs. Most of this area corresponds to older public parks and gardens (e.g., Crystal Palace Gardens and Passeio Alegre Garden; Figure 3.7), or old farms that have been converted into public parks more recently (e.g., Covelo Park and S. Roque Park; Figure 3.7), but some forestry still remains in the eastern and north-eastern parts of the city (particularly in the areas of Areosa and Areias; Figure 3.7). The inherent nature of forested areas, with periodic clearings and the use of monospecific cultures, can have negative effects on biodiversity levels (C. L. C. Liu et al., 2018; Pohjanmies et al., 2021), so its conservation value is probably limited. In contrast, the wooded habitat patches located in parks and gardens present a higher stability and are expected to harbour a more diverse and abundant array of species (Nielsen et al., 2014; Vasquez & Wood, 2022). Unlike what happened with the herbaceous cover, a significant amount of new TRS habitats was created between 1947 and 2019. This tree and shrub cover that developed more recently in vacant lots or previously cultivated land, with a multi-layered vegetation structure (which is not commonly observed in public parks and gardens) due to the lack of management, can also develop interesting levels of biodiversity, but faces additional challenges associated with the presence of invasive species, little social value and low acceptance by local residents (Filibeck et al., 2016; Gaertner et al., 2017).

The areas occupied with herbaceous (HER) cover have suffered a drastic reduction since 1947, which was particularly severe between 1979 and 2019; in the overall picture, around one third of the territory (1367 ha) experienced the loss of herbaceous habitats. The development of new built structures and impervious surfaces in Porto took the place of previously open spaces, which are usually covered with herbaceous vegetation, in a similar scenario as other geographic contexts (e.g. Tello et al., 2020). The creation of new herbaceous patches was insignificant (only 3.4% of the study area, 141 ha) and corresponds to areas where previously forested land was cleared for future urban development and areas where old industrial or residential urban fabric was demolished

and not yet replaced. Patches with persistent herbaceous vegetation occur in only 5.2% of the city (216 ha) and most of them express an agricultural past and were historically managed in the form of arable land or pastures. However, nowadays, most of these areas correspond to vacant lots without current defined use (where the herbaceous vegetation is kept by infrequent mowing or grazing), some have been absorbed by parks or gardens and converted to lawns, and only a small fraction retains an agricultural profile. The larger and older patches of herbaceous habitats are concentrated in the western extremity (the surrounding area of Nevogilde and Ervilheira streams), in the northern area (around Quinta da Prelada, Viso and Requesende), at the northeastern zone (around Contumil), and in the eastern portion of the city (particularly around the areas of Pinheiro de Campanhã, Tirares, Granja and Furamontes; Figure 3.7). Unlike most of the older wooded habitats, which are integrated in large parks and gardens, most of these old herbaceous patches are located in vacant lots and small cultivated areas, thus being quite vulnerable to being displaced by new urban developments.

In order to maintain sufficient levels of ecosystem functioning, to promote urban biodiversity and ultimately to benefit the health and well-being of the residents of Porto (Aerts et al., 2018; Pedersen Zari, 2018), vegetation patches and habitats should be preserved as they are becoming increasingly scarcer. Generally speaking, the biodiversity of different habitat types is enhanced when these habitats are older (Nordén et al., 2014), which can be due to a more complex vegetation structure and a more diverse collection of microhabitats that can harbour a higher diversity of species, as well as also factoring the time that certain species can take to colonize new habitat patches after dispersion (Janssen et al., 2017). The influence of habitat persistence varies according to several species life traits, especially their habitat specificity, longevity, and dispersal capability (Lira et al., 2019). Specialist, long-lived, and/or dispersal-limited species tend to show a more delayed response to habitat change (e.g. Krauss et al., 2010; Löfvenhaft et al., 2004; Sang et al., 2010). A similar pattern was discovered in a previous study focused on the patches conserving natural vegetation within the whole metropolitan area of Porto, where even small areas kept a substantial diversity of amphibian and reptile species with limited dispersal capabilities (Raquel Ribeiro, Sillero, et al., 2009). The maturity of vegetation, particularly trees, besides influencing the occurrence of microhabitat niches (Janssen et al., 2017), has also implications on the provision of several other ecosystem services beneficial for humans (Jonsson et al., 2020).

While the relationship between the age or continuity of urban habitats and their biodiversity levels is fairly understudied, several authors have investigated this association in other wooded and herbaceous habitats. It has been shown that forests and woodlands with a higher continuity in time exhibit a higher species richness, especially due to the occurrence of specialist species; these are associated with particular habitat niches that take time to develop as the forest stand matures, such as rough bark, tree cavities or deadwood (Janssen et al., 2017; Nordén et al., 2014; Siitonen & Saaristo, 2000). The city of Porto has, so far, succeeded at preserving a substantial portion of its older wooded habitats, by including them in public parks and gardens that provide multiple benefits for the citizens. A higher level of biodiversity in urban parks is positively associated with direct gains in the health and wellbeing of their users (Cameron et al., 2020; Schebella et al., 2019; Wood et al., 2018). Thus, in order to maximize the benefits of these old tree-covered habitats, it is necessary that their management considers the promotion of biodiversity and other ecosystem services. For example, it is important to allow trees to reach maturity, encourage the occurrence of multiple layers of vegetation and support the creation of diverse microhabitats, often contradicting traditional maintenance practices (Han et al., 2022; Le Roux et al., 2014; Nielsen et al., 2014; Threlfall et al., 2017).

Historical parks with restricted access, but belonging to institutions of public interest, have also an important role in the preservation of old woodlands in Porto, and they generally present lower disturbance levels due to reduced intensity of use. Here, this type of green space has its main origins in old recreational farms and manor house gardens and they can present a high biodiversity potential (Lõhmus & Liira, 2013). These areas are not publicly accessible, but are generally owned by institutions of public interest, such as universities, schools, health facilities, local government, etc. While these are likely to be maintained in the long run, their green spaces are not considered in spatial planning and are thus more susceptible to habitat destruction than public green spaces, and, consequently, its future preservation and adequate management should also be promoted. Likewise, some residential gardens are also relevant for the maintenance of older wooded habitats, especially near the city centre where the urban matrix is also from an earlier period. These areas also have biodiversity conservation interest, especially when considered collectively (Doody et al., 2010; Goddard et al., 2010; Thompson et al., 2003). These are particularly susceptible to urban development and, therefore, quite challenging to preserve. We suggest the engagement of the population towards biodiversity conservation practices and the implementation of

restrictions to further land development in these areas, accompanied by benefits for the involved homeowners (Goddard et al., 2010; Parris et al., 2018).

Similarly to wooded habitats, there is also a relation between herbaceous habitat age or continuity and its species richness (Inoue et al., 2021; Raduła et al., 2020), although it is still an understudied topic. In fact, herbaceous habitats, particularly grasslands, have been neglected by ecologists, land managers and planners, possibly due to the misconception that these are associated with land degradation after deforestation and other disturbances (Veldman et al., 2015). Urban grasslands are particularly affected and are often left out of conservation plans (Hüse et al., 2016). We have revealed a similar pattern in the city of Porto – while most of the relevant woodland patches have been safeguarded in parks and gardens, most of the old herbaceous patches have been lost due to urbanisation or lack of maintenance. As an exception, a few herbaceous patches have also been integrated in public parks (namely City Park and Oriental Park; Figure 3.7) and are likely to be maintained in the long run. However, these have been converted into lawns with dubious ecological value. The high frequency of mowing in these habitats is related to lower levels of plant, microorganism and invertebrate species richness (Chollet et al., 2018; Helden et al., 2018; Norton et al., 2019). The diversification of urban herbaceous habitats, so as to include different plant compositions, different heights and different uses, has the potential to generate considerable benefits for biodiversity. When adequately managed, urban herbaceous habitats, in the form of meadows, semi-natural grasslands, arable fields, etc., can provide valuable ecosystem services and harbour high biodiversity levels (Klaus, 2013; Onandia et al., 2019). Considering their extreme scarcity and lack of protection in the city of Porto, we believe that older herbaceous habitats should be considered as top priority regarding urban biodiversity conservation. To improve the biodiversity interest of herbaceous habitats in Porto, we suggest the promotion of a diverse vegetation community, aided by replanting native species and controlling invasive species, and the reinforcement of habitat connectivity amongst patches. The prospective loss of these vegetation patches at the city scale would contribute not only to the general trends of habitat destruction, but also to the trends of species extinctions that have already been described at an international level. For example, the European Environment Agency (2021) has recently reported the decline of farmland birds and grassland butterflies in EU member states, with both fauna groups being strongly associated with herbaceous habitats.

The most effective and cost-efficient strategy for urban habitat conservation involves the preservation of older habitat patches, but regeneration or restoration can be an

alternative or complementary solution (McKinney, 2002). When considering this solution, attention must be given to the history of former land uses of each targeted vegetation patch, as well as its landscape context, as they can influence the biodiversity outcomes and other ecosystem services (Foster et al., 2003; Vandewalle et al., 2014). Habitat restoration should also take advantage of spatial-temporal connectivity of the patch (Uroy et al., 2021; Zhao et al., 2021), i.e. the restored habitat should emerge at, or near, a place where that habitat type has occurred previously, to maximize the flow of biological resources to the new habitat patch. This is particularly important in the case of low habitat availability at a larger scale and for species with low dispersal capability (J.-L. Huang et al., 2020; Martensen et al., 2017). This way, older habitats, which can act as refuge for some species, can serve as a source for recolonization of the newly created favorable habitats.

The municipality of Porto has showed a growing interest in environmental issues in recent years, with plans to expand and connect its green infrastructure and with some interventions based primarily on the adaptation to climate change and, on a lesser degree, on the conflict between native and exotic species (Câmara Municipal do Porto, 2020b, 2021c, 2023). However, the long-term plan for biodiversity conservation is still to be concretized, as most goals, actions and timeframes are not explicit yet. Although there are prospects for creating new public green spaces, the prioritization criteria are not discernible. This research could serve as a starting point for the definition of a future habitat and biodiversity conservation plan or program, as it provides crucial information for habitat restoration or expansion in Porto and recommendations for the design and management of green areas. Figures 3.5 to 3.7 can help to identify priority areas for these types of interventions on wooded or herbaceous habitats, which should preferably occur near older vegetation patches, sites that have never been built and/or places where vegetation cover was recently lost.

The use of land cover trajectories seems to be an appropriate method to infer the degree of urban habitat continuity, with the main advantage of being a relatively simple and fast procedure, if adequate data is available, and that does not require expert knowledge. This method produces spatially explicit information, and its format has a high aptitude for the transfer of knowledge between the multiple actors in the design, planning and management of urban environments, from ecologists to landscape architects, urban planners, decision makers, and other stakeholders. For this exercise, we examined the evolution of land cover in Porto using three different time points, for a total period of 72 years. Although it was not possible due to limited resources and lack of available data,

for improved results we suggest expanding the timeframe into the past and using shorter time intervals, to better capture the rich history and the fast-paced dynamics of this urban area. This method of spatial prioritization for the conservation of urban habitats can be enriched with information about habitat structure, composition, species richness and abundance of multiple taxa. Other authors have also used habitat connectivity (Lv et al., 2019; Mollashahi et al., 2020; Zhao et al., 2021), climate beneficiation (Norton et al., 2015), social values (Whitehead et al., 2014) and biodiversity quality (Jalkanen et al., 2020) to define priority habitats in cities.

There are a multitude of factors influencing the outcome of land cover evolution in a city, but urban planning, design and management have a central role in paving the way for more biodiverse and sustainable cities (Hersperger et al., 2018; C.-W. Huang et al., 2018). City planners, designers and managers need to acknowledge that urban areas have the potential to harbour high levels of biodiversity and need to start integrating biodiversity concerns in their plans, policies and programs (Parris et al., 2018; Pedersen Zari, 2018). Planning, design and management decisions that affect the pattern and composition of the urban landscape can also impact urban biodiversity, and, hence, the quality of life of human urbanites (Pedersen Zari, 2018); it should be based on frequently updated and comprehensive information, displayed in a spatial framework, which must also include ecological data (Jarvis & Young, 2005). Similarly, ecologists need to address the needs of urban planners and managers regarding biodiversity conservation, translate them into ecologically relevant questions, and provide appropriate feedback that is useful at the scale of intervention (McDonnell & Hahs, 2013). Ultimately, the transformation of the urban landscape should be supported by multidisciplinary teams, but always including landscape and/or urban ecologists (Jarvis & Young, 2005; McDonnell & Hahs, 2013; Parris et al., 2018), so that science and research translates into real life practices and interventions, moving towards the greener, biodiverse and sustainable cities of the future.

## 3.6. Conclusion

Due to their nature, urban areas face a lack of vegetation, green spaces and habitats to support their biodiversity and ultimately the health and well-being of their citizens. In this study, we were able to identify the main urban habitat patches in the city of Porto, as well as their land cover history since the mid-20$^{th}$ century. Although around a third of the surface of the city is currently covered by vegetation, most of the vegetated patches have

experienced significant disturbance and frequent transformations between herbaceous and wooded habitats. Persistently wooded areas are rather scarce, but most are already protected in large parks and gardens. Areas continuously covered by herbaceous vegetation are even rarer in Porto and they are constantly disregarded by politicians, urban planners and even conservationists, being left out of urban planning and conservation programs.

Spatially explicit historical land cover data, such as the information presented here, can be easily integrated in spatial planning projects. It should, however, be complemented with more detailed information about habitat structure and species composition. We should aim to preserve, restore and, ideally, expand older habitats, whether occupied by trees, shrubs, or herbaceous vegetation. Older habitats allow for the formation of diverse microhabitats and the accommodation of diverse species over time, contributing for a richer biodiversity at the city or regional level. Regarding the dynamics of urban ecosystems, the conservation of herbaceous habitats seems to be particularly challenging. However, if managed properly, these habitats can provide fundamental ecosystem services and harbour important species that are becoming increasingly rare.

# Chapter 4.

# Mapping multigroup responses to land cover legacy for urban biodiversity conservation

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## 4.1. Abstract

Urban biodiversity plays a crucial role in the functioning of urban ecosystems and significantly impacts the well-being and quality of life for city residents. By focusing on the city of Porto as a case study, the influence of local-scale land cover evolution on urban biodiversity is investigated, using species richness of birds, reptiles, and amphibians as indicators, within a multimodel inference framework. The results underscore the importance of past land cover and land cover legacy in shaping urban biodiversity. Birds, reptiles, and amphibians respond positively to older vegetation patches but negatively to long-established urban areas. Birds exhibit adaptability by positively responding to recent vegetation, while amphibians tend to avoid newly vegetated zones. The fragmented distribution of amphibians and reptiles in Porto suggests limited mobility and a potential delayed response to habitat loss and isolation. Reptiles benefit from both wooded and herbaceous habitats, emphasizing the importance of local spatial diversity, while water elements are critical for amphibians, although many aquatic habitats in the urban context may not be suitable. Modelling results guide the identification of priority areas for urban biodiversity conservation in Porto, informing decision-makers, urban planners, and conservationists. This spatially explicit research aids efforts to create more ecologically resilient and biodiverse urban environments. It highlights the role of historical land cover and the unique responses of different vertebrate groups to urbanisation, contributing to our understanding of urban biodiversity dynamics and sustainable urban development.

**Keywords**: landscape change; local scale; multimodel inference; spatial prioritization; species richness; urban planning.

## 4.2. Introduction

Urban biodiversity is fundamental for urban ecosystem functioning (Harrison et al., 2014; Millennium Ecosystem Assessment, 2005; Pedersen Zari, 2018) and ultimately for the health, well-being, and quality of life of urban residents (Marselle et al., 2021). Cities are often located in biologically-rich areas (Ives et al., 2016; Kowarik, 2011) and urbanisation has detrimental effects on species and habitats (Fraissinet et al., 2023; Liang et al., 2023; McKinney, 2002; Simkin et al., 2022; Tilman et al., 2017). However, urban areas can

contribute to biodiversity conservation, as they often integrate a diverse mosaic of semi-natural and man-made habitats, home to unique assemblies of flora and fauna species, even including rare or threatened species (Jokimäki et al., 2018; Müller et al., 2013; Spotswood et al., 2021). Urbanisation is a complex and dynamic process, driven by a multitude of interacting social, economic, and environmental factors (Shaw et al., 2020). Land cover change is one of its main consequences, often resulting in the loss and fragmentation of vegetation, natural or semi-natural habitats, and agricultural land (Güneralp et al., 2020; Richards & Belcher, 2020), with deleterious effects on local species communities (Callaghan et al., 2021; Concepción et al., 2015; Ross & Henkanaththegedara, 2019).

Urban species assemblies are the result of the interaction between landscape heterogeneity and connectivity, which depend on the age and history of each site or habitat patch (Alberti et al., 2020; Alberti & Wang, 2022; M. L. Cadenasso et al., 2006; Foster et al., 2003). While this topic remains relatively understudied in urban contexts, several authors have investigated the relationship between persistence or age of different types of habitats and their biodiversity levels, in other ecosystems. In general, older habitats, i.e. those that are persistent in time and have experienced less changes, exhibit higher levels of biodiversity (Janssen et al., 2017; Nordén et al., 2014; Raduła et al., 2020). Habitat persistence can influence the occurrence of diverse organismal groups over time, by interfering with different ecological processes. For instance, by generating time-lagged responses, it affects metapopulation and metacommunity dynamics, such as dispersal, (re)colonization, and extinction; this can lead to phenomena of extinction debt or immigration (or species) credit (Lira et al., 2019; Swan et al., 2021; Uroy et al., 2021). Additionally, persistent or older habitats usually present a more complex vegetation structure and a more diverse collection of habitat niches that take time to develop in the ecological succession, such as tree cavities or wood decay, creating favourable conditions for a higher diversity of organisms, particularly specialist species (Janssen et al., 2017; Nordén et al., 2014). Species life-history traits determine their different responses to land cover change and persistence, namely their habitat specificity of different life stages, longevity, and dispersal capability (Lindenmayer et al., 2023; Lira et al., 2019). Species that are habitat specialists at any life stage, long-lived, and with restricted dispersal, tend to show a more delayed response (e.g. Krauss et al., 2010; Löfvenhaft et al., 2004; Sang et al., 2010) and are, thus, more susceptible to environmental change. For these reasons, habitat age or persistence can be considered as a good indicator of urban biodiversity value and be can used to inform urban habitat

conservation programs, as well as to support evidence-based decision-making regarding urban landscape planning, design and management (Jarvis & Young, 2005; Wittig & Schreiber, 1983).

The complexity and heterogeneity of the urban territory translate into additional challenges for spatial planning and management (Borgström et al., 2006), taking into consideration the intricate fabric of greener areas amidst a more artificial matrix. The ecological dynamics of the urban landscape is largely affected by local-scale decisions and interventions, related to the planning and design of individual sites, infrastructures, and community masterplans (Brown, 2017). Beyond the cooperation between multiple disciplines and stakeholders, data collection and spatial analysis must contribute to the integration of ecological information in urban planning, design, and management, i.e., generate "actionable knowledge" (Garrard et al., 2018; Zhou et al., 2019). The scale of analysis is particularly important when considering urban biodiversity preservation – the local scale is more closely related to the planning and management decisions that directly translate into site interventions that modify urban habitats (Ancillotto et al., 2019; Brown, 2017; Łopucki & Kiersztyn, 2015; Molné et al., 2023; Opdam et al., 2013).

In urban areas there is a generalized lack of data on species occurrence and abundance, which is even more severe at the local scale (Grafius et al., 2019) and for certain taxa, such as amphibians, reptiles, bats and particular groups of invertebrates (Faeth et al., 2011; Rega-Brodsky et al., 2022). When it comes to urban vertebrates, birds are the main choice for most researchers – they are good indicators of urban ecosystem condition, providing cheap and easy measurements, and are sensitive to changes in habitat structure and composition (Farinha-Marques et al., 2011). In contrast, urban herpetofauna (amphibians and reptiles) is poorly studied and needs a thorough analysis (Faeth et al., 2011; Rega-Brodsky et al., 2022) with most species being highly susceptible to local habitat transformation and fragmentation (Cordier et al., 2021; Delaney et al., 2021), phenomena that are especially noticeable in urban areas (Niemelä, 2011).

The scientific evidence coming from landscape ecology lays the groundworks for understanding the relationship between biodiversity and the spatially explicit environment in which it occurs in a given timeframe. Ecological modelling is a fundamental tool to predict the spatial variation in biodiversity, which is particularly useful in a context of high spatial complexity and heterogeneity, such as urban areas (Grafius et al., 2019). Spatial predictions can also be useful to tackle lack of biodiversity data in some locations. In urban biodiversity research, modelling analysis is often used to study

the occurrence of particular species (e.g. Plummer et al., 2020) or patterns of species richness (e.g. Petersen et al., 2020).

In this article, we aim to investigate how the evolution of land cover, at a local scale, influences urban biodiversity. Using vertebrate species richness as an indicator of biodiversity levels, we test the influence of: 1) water elements, 2) current land cover, 3) past land cover, 4) age of vegetation cover, and 5) trend of vegetation cover change, on biodiversity, using a multimodel inference framework. Based on the results of species richness modelling, with the intent of producing "actionable knowledge", we aim to identify priority areas for the conservation of urban biodiversity for the case of Porto, Portugal. Based on the abovementioned literature and on the knowledge of the system, we hypothesize that all studied animal groups (birds, reptiles and amphibians) are influenced by the current land cover and also reveal a response to land cover legacy (e.g., higher richness with more temporal stability), possibly in different forms due to life-history. Moreover, we predict that herpetofauna will display a stronger response to land cover change than birds, being more associated with older habitats, due to their limited dispersal capabilities; amphibians are also expected to present a stronger relationship with the presence of water, due to their life cycle requirements. If our expectations are met, urban planning and management needs to prioritize the preservation and expansion of the older habitat areas.

## 4.3. Methods

### *4.3.1. Study area*

This research was conducted in Porto, a city located at the intersection of the Douro River with the Atlantic Ocean, in Northern Portugal (Figure 4.1). Porto is a densely urbanised, medium-sized city (with around 42 $km^2$ and almost 232,000 inhabitants; INE, 2022) and it is at the core of a dynamic metropolitan area, comprised of 17 municipalities and around 1.7 million residents (AMP, 2022). The city benefits from a mild temperate climate (*Csb* regime, Koppen-Geiger classification; Peel et al., 2007); the latest climate records indicate a mean annual temperature of 15.3°C and annual precipitation of 1174.0 mm (data for 2021; PORDATA, 2022).

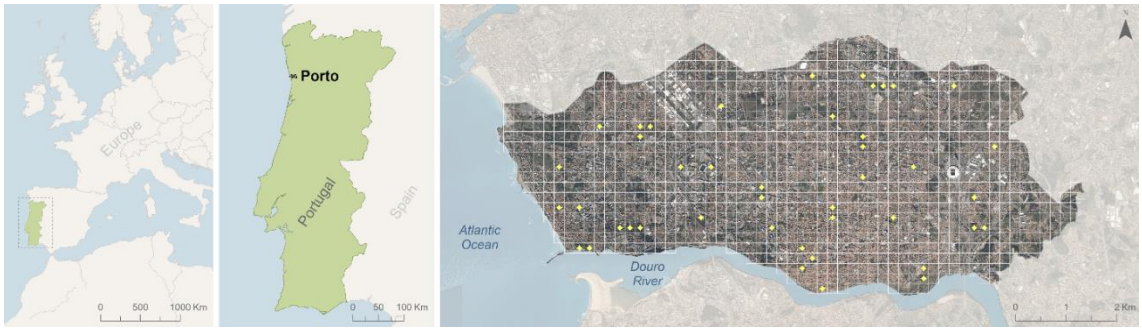



**Figure 4.1.** Location of the study area (Porto, Portugal), and the selected squares for fauna sampling (yellow marks).

Porto has experienced a dynamic land cover evolution in the recent past. While most of the territory was occupied by vegetation in 1947 (63.6% cover), it has suffered a drastic increase in urbanised areas that completely dominate the territory in 2019 (62.5% cover; Guilherme et al., 2022). For the purpose of fauna survey and species distribution modelling, the study area was divided with a 200×200m grid, originating 994 squares (those that included <50% of municipal land were excluded).

### *4.3.2. Response variables*

For the assessment of urban fauna species, 43 of the 200×200m squares were selected to survey three groups of vertebrates: birds, reptiles, and amphibians (Figure 4.1). The selection of the squares was made in order to capture the main trends of land cover evolution occurring in Porto since the mid-20$^{th}$ century (Guilherme et al., 2024).

The presence of birds, reptiles, and amphibians was recorded during the spring and summer (April to July) of 2019 and 2021. Birds were surveyed using visual and acoustic detection and identification, with point-counts of eight minutes, between 6.30 and 9.00 a.m., as near as possible to the centre of the selected square (Rabaça, 1995; Sutherland et al., 2004). Only individuals which were explicitly using the site were recorded, i.e., birds that only flew over were not associated with the surveyed square (Huff et al., 2000). Reptiles and amphibians were surveyed through directed visual transects and refugia searching in the entire square; additionally, if water elements were present, netting was also used as a method to detect the larval stages of amphibians (Heyer et al., 1994; McDiarmid et al., 2014; Sewell et al., 2013). After evaluating the species accumulation curves for each site, bird surveys were performed six times in each square, while reptiles and amphibians were searched during four visits. This sampling intensity ensured saturation of species richness curves in this area (Farinha-Marques et al., 2023; Raquel

Ribeiro, 2011). Finally, species richness was estimated for each of the fauna groups in the selected squares. This information was used to assess how land cover evolution affects species richness through a modelling framework.

### *4.3.3. Predictor variables*

For the purpose of this study, predictors concern multiple sets of variables related to different land cover categories of the city of Porto and their evolution between three different time periods: 1947, 1979, and 2019, based on the work of Guilherme et al. (2024). The mentioned research relied on the mapping of land cover in vectorial format in a GIS environment, following visual interpretation of remote sensing data (historic aerial photograph and satellite imagery), considering a minimum area of 2000 $m^2$ and a minimum width of 5m. For the three dates (1947, 1979, and 2019), the study area was mainly distinguished in two broad categories: vegetated and non-vegetated areas. Vegetated areas were further segregated into tree and shrub cover (TRS) and herbaceous cover (HER). Non-vegetated areas were covered by artificial built elements (ABE), aquatic surfaces (AQU), or bare soil, sand, rock, or other sediment (SPV); only ABE was considered in the present work, as AQU and SPV play a reduced role in the land cover evolution in Porto.

The classification and mapping of the land cover of Porto for these three dates allowed for the assessment of the main changes in vegetation patches in terms of persistence, gain or loss, as well as the inference of the approximate age of each vegetation patch in three intervals: 0 to 39 years, 40 to 71 years, and 72 years or more.

Due to their importance for amphibians, and although they were not included as a measure of cover, the presence of water elements was considered as a predictor variable in a binary form, as most small-scale water features in this dense urban context were not adequately captured with the standard land cover mapping procedures.

To assess how different spatial scales can influence the distribution of different animal groups, all predictor variables were calculated considering two versions: 1) for each 200×200m square, and 2) for a buffer of 200m around each square (approximately a 600×600m square). The 200×200m square (hereafter named fine scale) is strongly related to the site scale and is associated with the home range and dispersal distances of the less mobile species of amphibians (Trochet et al., 2014), while the 600×600m square (coarse scale) corresponds to the neighbourhood scale and includes the

dispersal range of common reptile species (A. Grimm et al., 2014). All bird species in the study area are expected to easily surpass these distances.

Groups of predictor variables, in both scales, were used to inform different models; the complete list of models and descriptions of predictor variables is explained in Table 4.1. Predictors with Spearman correlation coefficient ≥0.7 were excluded from the same model to avoid multicollinearity issues (Daoud, 2017; Guisan & Zimmermann, 2000; Shrestha, 2020).

### *4.3.4. Modelling framework*

To evaluate the effect of several land cover predictors on the species richness of birds, reptiles, and amphibians, the data analysis was organized according to five hypotheses: 1) presence of water; 2) current land cover; 3) past land cover; 4) age of vegetation cover; 5) trend of vegetation cover. Each of these hypotheses originated several groups of predictor variables, totalling 32 models (Table 4.1). We fit this set of competing models within a multimodel inference (MMI) framework to assess how well each model was supported by the data, instead of using a single best model (Burnham & Anderson, 2002). This allowed a direct comparison and a better assessment of the relative contribution of the influence of several land cover factors on the species richness of the different groups of animals under study. A null model (intercept model), assuming that all locations have the same probability of having the same species richness, i.e., that the land cover evolution does not affect species richness, was included as a sixth hypothesis (Table 4.1) in all analyses. This allowed testing whether the competing models for the previous hypotheses are more reliable than an intercept model (Burnham & Anderson, 2002).

**Table 4.1.** List of hypotheses, competing models and predictors used in the multimodel inference framework.

| Hypothesis | Competing models | Predictors |
|---|---|---|
| ***Water elements*** (Chamberlain et al., 2007; Mbiba et al., 2021) | M1, M2: Water | Water (presence of water elements in 2019) |
| ***Current land cover*** (Amaya-Espinel et al., 2019; Aronson et al., 2014) | M3, M4: Type of vegetation cover in 2019 | TRS2019 (% tree and shrub cover in 2019)<br>HER2019 (% herbaceous cover in 2019) |
| | M5, M6: Vegetation cover in 2019 | Veg2019 (% vegetation cover in 2019) |
| | M7, M8: Artificial cover in 2019 | ABE2019 (% artificial cover in 2019) |
| ***Past land cover*** (Foster et al., 2003; Tello et al., 2020) | M9, M10: Type of vegetation cover in 1979 | TRS1979 (% tree and shrub cover in 1979)<br>HER1979 (% herbaceous cover in 1979) |
| | M11, M12: Vegetation cover in 1979 | Veg1979 (% vegetation cover in 1979) |
| | M13, M14: Artificial cover in 1979 | ABE1979 (% artificial cover in 1979) |
| | M15, M16: Type of vegetation cover in 1947 | TRS1947 (% tree and shrub cover in 1947)<br>HER1947 (% herbaceous cover in 1947) |
| | M17, M18: Vegetation cover in 1947 | Veg1947 (% vegetation cover in 1947) |
| | M19, M20: Artificial cover in 1947 | ABE1947 (% artificial cover in 1947) |
| ***Age of vegetation cover*** (Barth et al., 2015; Fernández-Juricic, 2000; C. A. McAlpine et al., 2015) | M21, M22: Age of tree and shrub cover | TRS72y (% tree and shrub cover existing for 72 years or more)<br>TRS4071y (% tree and shrub cover existing for 40 to 71 years)<br>TRS039 (% tree and shrub cover existing for less than 39 years) |
| | M23, M24: Age of herbaceous cover | HER72y (% herbaceous cover existing for 72 years or more)<br>HER4071y (% herbaceous cover existing for 40 to 71 years)<br>HER039y (% herbaceous cover existing for less than 39 years) |
| | M25, M26: Age of vegetation cover | Veg72y (% vegetation cover existing for 72 years or more)<br>Veg4071y (% vegetation cover existing for 40 to 71 years)<br>Veg039y (% vegetation cover existing for less than 39 years) |

**Table 4.1**. (continued)

| Hypothesis | Competing models | Predictors |
|---|---|---|
| ***Trend of vegetation cover change*** (Fraissinet et al., 2023; Knick & Rotenberry, 2000) | M27, M28: Tree and shrub cover change | TRS72y (% tree and shrub cover existing for 72 years or more)<br>TRSLoss (% tree and shrub cover lost between 1947 and 2019)<br>TRSGain (% tree and shrub cover gained between 1947 and 2019, where it did not occur before)<br>TRSDisturb (% tree and shrub cover gained between 1979 and 2019, in a location where it occurred in 1947) |
| | M29, M30: Herbaceous cover change | HER72y (% herbaceous cover existing for 72 years or more)<br>HERLoss (% herbaceous cover lost between 1947 and 2019)<br>HERGain (% herbaceous cover gained between 1947 and 2019, where it did not occur before)<br>HERDisturb (% herbaceous cover gained between 1979 and 2019, in a location where it occurred in 1947) |
| | M31, M32: Vegetation cover change | Veg72y (% vegetation cover existing for 72 years or more)<br>VegLoss (% vegetation cover lost between 1947 and 2019)<br>VegGain (% vegetation cover gained between 1947 and 2019, where it did not occur before)<br>VegDisturb (% vegetation cover gained between 1979 and 2019, in a location where it occurred in 1947) |
| ***Null model*** (Burnham & Anderson, 2002) | M33: null model | |

We used the corrected Akaike information criterion (AIC; Akaike, 1973) for small sample sizes ($AIC_c$), as recommended when the ratio between $n$ (the number of observations used to fit the model) and $K$ (the number of parameters in the largest model) is < 40 (Burnham & Anderson, 2002; Shono, 2000). We also limited the maximum number of predictors per model to four because of small sample sizes. For comparing among models, we calculated the $AIC_c$ difference, where $\Delta_i = AIC_c\ i - AIC_c\ min$ (Burnham & Anderson, 2002). Values of $\Delta_i \leq 2$ indicate models with good performance, while models with $\Delta_i < 7$ can be considered acceptable, although less supported by the data (Burnham & Anderson, 2002). These differences ($\Delta_i$) were used to derive Akaike weights ($w_i$), which represent the probability that a candidate model will be the best approximating and most parsimonious model given the data and set of models. Akaike weights are scaled

between zero and one and represent the proportional support for a particular model given all models. Additionally, we calculated the adjusted $R^2$ to estimate the models' explanatory power (Guisan & Zimmermann, 2000).

In a subsequent step, all models performing worse than the null model were discarded, and we calculated the average model and the averaged parameter estimates, weighted by the corrected $w_i$ values. Finally, the average model for each fauna group was used for spatial prediction of species richness in the complete study area. This information was then used to determine the priority areas for biodiversity conservation in Porto.

All models were fit using Generalized Linear Models (GLMs) in R, version 4.2.3 (R Core Team, 2023), with the aid of the packages "AICcmodavg" (Mazerolle, 2023) and "rms" (Harrell, 2023). Species richness (for the three different animal groups) was used as the response variable in GLMs with Poisson variance and log link function (Guisan & Zimmermann, 2000; Vincent & Haworth, 1983). The code used in R for the modelling framework has been previously applied by Vicente et al. (2014; see Appendices for the full R script).

## 4.4. Results

### *4.4.1. Species richness of birds*

Bird surveys revealed a total of 40 bird species across the study area; species richness in each site varied from 6 to 24 (supplementary material, chapter 4.7.1). The multimodel inference showed substantial model selection uncertainty, suggested by the low Akaike weights ($w_i$; Table 4.2). It should be noted that the large number of tested models can contribute to lower $w_i$ values.

Nevertheless, among the analysed predictors, artificial (ABE) and vegetation (Veg) cover seem to have a larger effect on bird species richness, especially at a smaller spatial scale. Although the current land cover has a relevant impact on bird species richness (ABE2019 and Veg2019), the land cover legacy was also evident, as the different land cover types recorded for 1947 (ABE1947 and Veg1947) contribute to some of the best models (Table 4.2). In general, artificial land cover has a negative effect on the species richness of birds (particularly ABE2019 and ABE1947), whereas vegetation cover has a positive effect (Veg2019, Veg1947). The model regarding vegetation cover change was one of the most important, but its results can be difficult to interpret, as bird species

richness seems to be positively associated with all vegetated areas, as well as areas that experienced vegetation loss. However, areas that went through a recent increase in vegetation cover (VegGain and VegDisturb) appear to have a particularly positive impact on bird species richness. The age of vegetation cover does not seem to have an important influence on bird species richness, nor does the presence of water elements.

**Table 4.2**. Results of information-theoretic-based model selection and multimodel inference for bird species richness, showing the number of parameters (*K*), AIC difference ($\Delta_i$ ), Akaike weights ($w_i$), adjusted $R^2$, predictors, and their effect on bird species richness. Only the 10 best models are shown, for complete results see Table 4.7 in supplementary material, chapter 4.7.2.

| Model | *K* | $\Delta_i$ | $w_i$ | adj. $R^2$ | predictors | effect |
|---|---|---|---|---|---|---|
| M19: Artificial cover in 1947 (fine scale) | 3 | 0 | 0.152082 | 0.235324 | ABE1947F | negative |
| M7: Artificial cover in 2019 (fine scale) | 3 | 0.039688 | 0.149094 | 0.234169 | ABE2019F | negative |
| M5: Vegetation cover in 2019 (fine scale) | 3 | 0.619803 | 0.111555 | 0.217284 | Veg2019F | positive |
| M18: Vegetation cover in 1947 (coarse scale) | 3 | 1.031569 | 0.090798 | 0.205298 | Veg1947C | positive |
| M17: Vegetation cover in 1947 (fine scale) | 3 | 1.055675 | 0.08971 | 0.204597 | Veg1947F | positive |
| M31: Vegetation cover change (fine scale) | 6 | 1.271058 | 0.080551 | 0.36497 | Veg72yF<br>VegDisturbF<br>VegGainF<br>VegLossF | positive<br>positive<br>positive<br>positive |
| M20: Artificial cover in 1947 (coarse scale) | 3 | 2.41604 | 0.04544 | 0.165001 | ABE1974C | negative |
| M3: Type of vegetation cover in 2019 (fine scale) | 4 | 2.870273 | 0.036208 | 0.199652 | TRS2019F<br>HER2019F | positive<br>positive |
| M16: Type of vegetation cover in 1947 (coarse scale) | 4 | 2.911869 | 0.035463 | 0.198411 | TRS1947C<br>HER1947C | positive<br>positive |
| M15: Type of vegetation cover in 1947 (fine scale) | 4 | 3.088168 | 0.032471 | 0.193152 | TRS1947F<br>HER1947F | positive<br>positive |

### *4.4.2. Species richness of reptiles*

During reptile surveys, four species were identified in the selected sampling sites. Species richness varied between 0 and 2; the presence of reptiles was only detected in around half of the sites (supplementary material, chapter 4.7.1).

Despite the model selection uncertainty, current vegetation cover (Veg2019, TRS2019, and HER2019) seems to have a predominant effect on reptile species richness,

especially at a coarse scale (Table 4.3). To a lesser degree, there seems to be an influence of past land cover at different temporal and spatial scales, with past vegetation cover (Veg1979 and Veg1947) being associated with an increase in species richness and past artificial cover (ABE1979 and ABE1947) with a decrease in species richness. Although some effects of land cover legacy (past land cover) can be discerned, the age of vegetation cover and the trend of vegetation cover evolution, as well as the presence of water, do not seem to play a significant role in shaping reptile species richness.

**Table 4.3.** Results of information-theoretic-based model selection and multimodel inference for reptile species richness, showing the number of parameters (*K*), AIC difference ($\Delta_i$ ), Akaike weights ($w_i$), adjusted $R^2$, predictors and their effect on reptile species richness. Only the 10 best models are shown, for complete results see Table 4.8 in supplementary material, chapter 4.7.2.

| Model | *K* | $\Delta_i$ | $w_i$ | adj. $R^2$ | predictors | effect |
|---|---|---|---|---|---|---|
| M6: Vegetation cover in 2019 (coarse scale) | 3 | 0 | 0.308051 | 0.328195 | Veg2019C | positive |
| M4: Type of vegetation cover in 2019 (coarse scale) | 4 | 2.298104 | 0.097633 | 0.31194 | TRS2019C<br>HER2019C | positive<br>positive |
| M14: Artificial cover in 1979 (coarse scale) | 3 | 2.565197 | 0.085427 | 0.249839 | ABE1979C | negative |
| M11: Vegetation cover in 1979 (fine scale) | 3 | 2.754337 | 0.077719 | 0.244061 | Veg1979F | positive |
| M20: Artificial cover in 1947 (coarse scale) | 3 | 3.46306 | 0.054529 | 0.222413 | ABE1947C | negative |
| M17: Vegetation cover in 1947 (fine scale) | 3 | 3.818592 | 0.045648 | 0.211553 | Veg1947F | positive |
| M12: Vegetation cover in 1979 (coarse scale) | 3 | 4.239417 | 0.036987 | 0.198698 | Veg1979C | positive |
| M19: Artificial cover in 1947 (fine scale) | 3 | 4.255886 | 0.036683 | 0.198195 | ABE1947F | negative |
| M13: Artificial cover in 1979 (fine scale) | 3 | 4.470407 | 0.032952 | 0.191642 | ABE1979F | negative |
| M5: Vegetation cover in 2019 (fine scale) | 3 | 4.547676 | 0.031704 | 0.189282 | Veg2019F | positive |

### *4.4.3. Species richness of amphibians*

Amphibians are one of the rarest vertebrate groups in the city of Porto. Although five species were detected, amphibians were only present in 6 of the 43 sampling sites (supplementary material, chapter 4.7.1). The zero-inflated data may have influenced the results of the multimodel inference, as most of the models for amphibians perform poorly in explaining the variation in species richness (high values of $\Delta_i$; Table 4.4).

Nevertheless, the analysis suggests that the presence of water is the most important determinant of amphibian species richness (Table 4.4), as would be expected; this effect is particularly noticed at a finer scale.

Besides water, vegetation cover and tree and shrub cover (TRS) also seem to have an influence; the effect of land cover legacy can be seen in this group, as past vegetation patterns contribute to some of the best models (TRS1979, HER1979, TRS1947, HER1947), but not current vegetation cover. Of the studied groups, amphibians were the only to exhibit an obviously different response to TRS and HER cover: the number of species is positively influenced by TRS cover, while it is negatively related to HER cover at multiple temporal scales and particularly at a coarser resolution.

**Table 4.4.** Results of information-theoretic-based model selection and multimodel inference for amphibian species richness, showing the number of parameters (*K*), AIC difference ($\Delta_i$ ), Akaike weights ($w_i$), adjusted $R^2$, predictors and their effect on amphibian species richness. Only the 10 best models are shown, for complete results see Table 4.9 in supplementary material, chapter 4.7.2.

| Model | *K* | $\Delta_i$ | $w_i$ | adj. $R^2$ | predictors | effect |
|---|---|---|---|---|---|---|
| M1: Water (fine scale) | 3 | 0 | 0.738084 | 0.396837 | WaterF | positive |
| M25: Age of vegetation cover (fine scale) | 5 | 3.82287 | 0.109139 | 0.389546 | Veg72yF<br>Veg4071yF<br>Veg039yF | positive<br>positive<br>negative |
| M10: Type of vegetation cover in 1979 (coarse scale) | 4 | 6.361833 | 0.030666 | 0.281446 | TRS1979C<br>HER1979C | positive<br>negative |
| M28: Tree and shrub cover change (coarse scale) | 6 | 6.819777 | 0.02439 | 0.362315 | TRS72yC<br>TRSDisturbC<br>TRSGainC<br>TRSLossC | positive<br>negative<br>positive<br>negative |
| M2: Water (coarse scale) | 3 | 7.354496 | 0.018668 | 0.218965 | WaterC | positive |
| M22: Age of tree and shrub cover (coarse scale) | 5 | 7.692374 | 0.015766 | 0.291161 | TRS72yC<br>TRS4071yC<br>TRS039yC | positive<br>positive<br>negative |
| M9: Type of vegetation cover in 1979 (fine scale) | 4 | 8.134968 | 0.012636 | 0.23749 | TRS1979F<br>HER1979F | positive<br>positive |
| M31: Vegetation cover change (fine scale) | 6 | 8.310177 | 0.011576 | 0.323423 | Veg72yF<br>VegDisturbF<br>VegGainF<br>VegLossF | positive<br>negative<br>positive<br>positive |
| M16: Type of vegetation cover in 1947 (coarse scale) | 4 | 9.115074 | 0.007741 | 0.213193 | TRS1947C<br>HER1947C | positive<br>negative |
| M21: Age of tree and shrub cover (fine scale) | 5 | 9.5757647 | 0.0061483 | 0.2432741 | TRS72yF<br>TRS4071yF<br>TRS039yF | positive<br>positive<br>negative |

The age of vegetation cover is also integrated into the best models for determining species richness: a higher number of amphibian species seems to be associated with older habitat patches (Veg72y, Veg4071y, TRS72y, TRS4071y), while recent patches have lower species richness (Veg039y, TRS039y). Regarding the evolution trend of the vegetation cover, the patterns are unclear, but, again, a higher number of species seems to be located in areas with more persistent tree and shrub cover (TRS72y).

### *4.4.4. Spatial prediction and identification of priority areas*

Spatial predictions from the average models for each fauna group (after the exclusion of the worst models) are presented in Figure 4.2. For birds, the average model predicts values from 12 to 20 species. The lowest values are concentrated in the city centre, in the south, where artificial cover is higher and vegetation cover is lower. The highest values of predicted bird species richness are located in the periphery, especially at the western and eastern extremities. Reptiles present a similar pattern, where the central core of the study area has lower values of species richness (predicted value of zero), and the periphery is predicted to be slightly more diverse (1 or 2 species). The modelling results show a particularly unfavourable scenario for amphibians: most of the city is predicted to have zero species, with only a few isolated squares portraying the presence of one species.

The results of the multimodel inference and the spatial predictions were used to evaluate the priority level for the entire study area regarding the conservation of urban biodiversity, according to the criteria presented in Table 4.5. This approach favours sites with the highest number of species (predicted or observed) for all analysed groups, as can be seen in Figure 4.3.

**Table 4.5.** Criteria for the determination of the priority level according to values of species richness (observed values for sampled squares, predicted values for unsampled sites).

| **Priority level** | **Species richness criteria** | | | | |
|---|---|---|---|---|---|
| | **Amphibians** | | **Reptiles** | | **Birds** |
| Top priority | ≥ 1 | or | ≥ 2 | or | ≥ 19 |
| High priority | 0 | and | 1 | and | 17-18 |
| Medium priority | 0 | and | 1 | and | ≤ 16 |
| | 0 | and | 0 | and | 17-18 |
| Low priority | 0 | and | 0 | and | ≤ 16 |

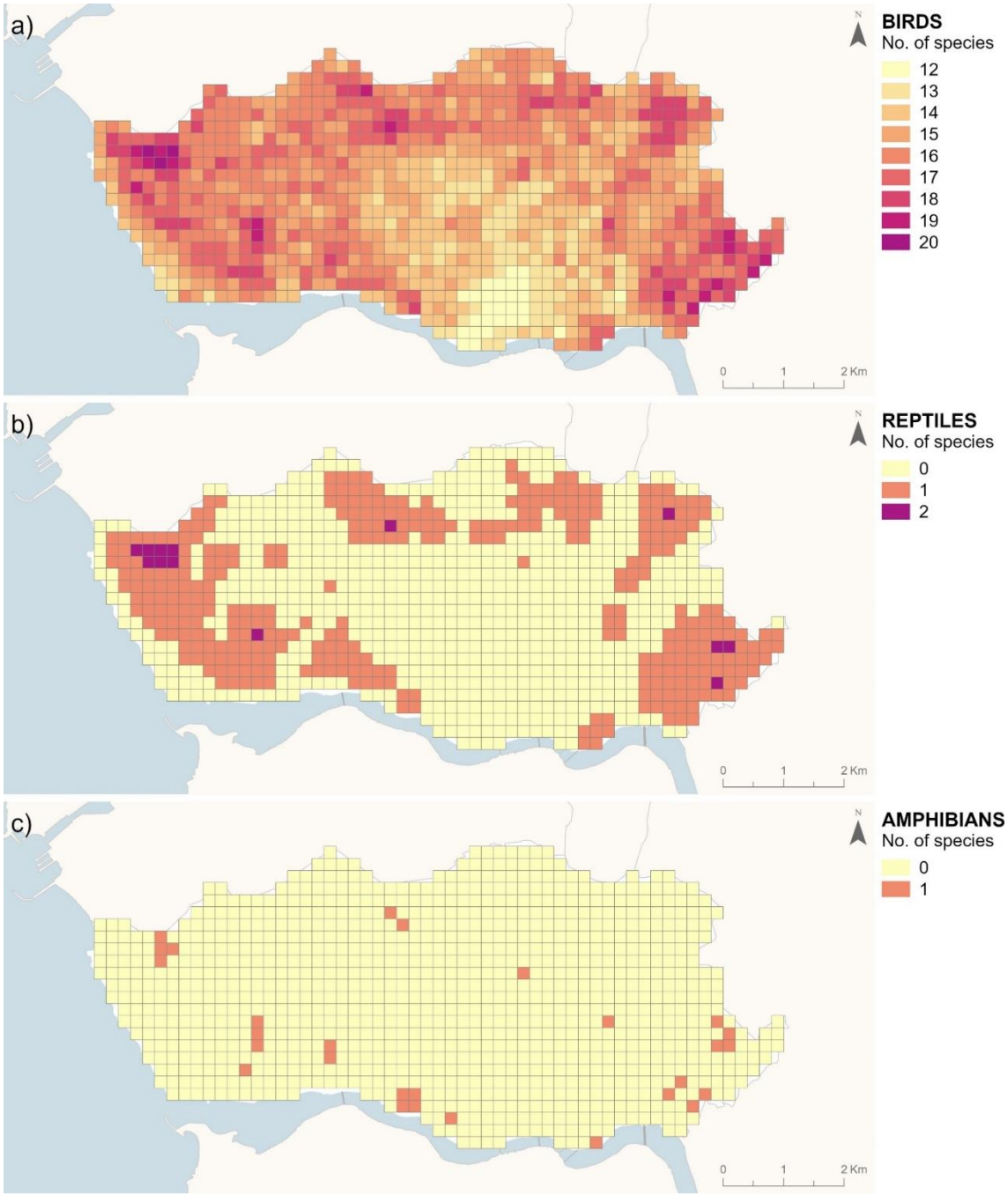



**Figure 4.2.** Spatial prediction for the species richness of birds (a), reptiles (b), and amphibians (c), obtained from the average models.

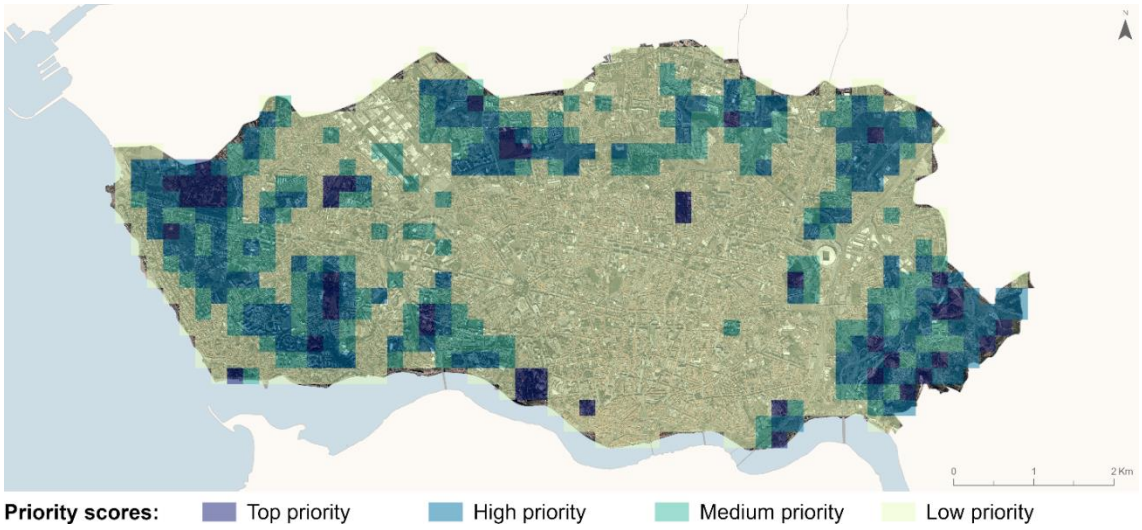



**Figure 4.3.** Priority areas for the conservation of urban biodiversity in Porto, based on the effects of land cover evolution on species richness (background imagery: Direção Geral do Território, 2018).

## 4.5. Discussion

### *4.5.1. Species richness of birds*

Bird species richness in Porto seems to exhibit a positive relation with vegetated areas and a negative relation with built-up or impervious areas, in accordance to other studies (e.g., Amaya-Espinel et al., 2019; Carbó-Ramírez & Zuria, 2011; Humphrey et al., 2023). However, the adverse effect of the artificialization of the territory appears to extend here into the past, as the areas urbanised for over 72 years tend to have fewer species (e.g., near Infante D. Henrique Square and República Square). Results also suggest a legacy effect of vegetation cover, since a higher number of species persist in or close to areas vegetated in 1947, even if a large portion of vegetation cover was lost nearby (e.g., near Francisco Sá Carneiro Square and Ramalde Sports Park).

Conversely, bird species also seem to positively respond to recent vegetation cover, highlighting their high mobility and dispersal abilities that allow them to easily colonize new habitats (Lens et al., 2002) and to quickly respond to habitat changes (Atwell et al., 2012; Audet et al., 2016). In Porto, this response is associated with the creation of new green spaces that replace previously urbanised locations (e.g., Machado de Assis Garden and Sophia's Garden) and with vegetation growth in newly urbanised areas that substituted previous agricultural fields and forest patches (e.g., near Paulo Vallada Garden and Ramalde Sports Park).

Contrary to other studies (Barth et al., 2015; Fernández-Juricic, 2000), we were not able to detect a relevant influence of the age of vegetation cover on bird species richness. The use of species richness as the response variable can mask certain factors affecting particular species, especially considering the difference in habitat suitability for specialist and generalist species (Connor et al., 2018). As often reported in urban contexts, a large portion of the sampled birds in Porto corresponds to generalist and opportunistic species (such as *Turdus merula* or *Pica pica*). Only a fraction is composed of habitat specialists (forest species, such as *Certhia brachydactyla*, or grassland species, such as *Cisticola juncidis*), which tend to be associated with particular habitat niches (Connor et al., 2018) and older vegetation patches (Nordén et al., 2014). Similarly, aquatic bird species were virtually absent from most sampled sites, which can help explain why water elements did not present a relevant influence on species richness, contradicting other studies (e.g., Mbiba et al., 2021). Habitat specialists may not contribute to a significant increase in the number of species at each site, but their presence in particular locations strengthens the species richness at the city level.

Regarding the scale of analysis, birds seem to exhibit a stronger response to predictor variables measured at finer scales. This may be due to a higher detectability of birds in sites where they nest or feed, compared to sites mainly used for dispersal, typically examined at coarser scales. Alternatively, the prevalence of generalist species on the city species pool may generate a stronger link with the fine scale, as they tend to disperse less than specialist species (Martin & Fahrig, 2018; Neuschulz et al., 2013).

Although the average model was not able to precisely predict the observed bird species richness (ranging from 6 to 24 species per site), it generated a spatial pattern that is relatively close to reality. As exposed by the model spatialization, the city centre, particularly the historic/medieval part, is relatively poor in bird species, with only opportunistic bird species persisting, nesting directly in buildings (e.g., *Columba livia*, *Larus michahellis*, *Passer domesticus*), due to the lack of diverse vegetated habitats. Predicted species richness of birds is concentrated in the city's periphery, where most large vegetation patches occur (e.g., City Park, Serralves Park, Prelada Park, Oriental Park, and the areas of Ervilheira/Nevogilde, Asprela, Contumil/Currais, Rio Tinto and Rio Torto). The peripheral arc was almost completely rural and semi-natural from 1947 to 1979, while the city centre was already covered by a dense urban fabric in 1947.

### *4.5.2. Species richness of reptiles*

The city of Porto harbours relatively few species of reptiles; the wall lizard (*Podarcis bocagei*) is the most prevalent throughout the study area, while others occur only in isolated locations scattered throughout the territory. The low abundance and diversity of this vertebrate group, along with the generic habitat requirements of the most common species, could help explain the modest performance of most models ($\Delta_i$ >2). Nevertheless, the modelling framework reveals interesting patterns of reptile distribution within the city (Ackley et al., 2015; García-París & Martín, 1987; Rugiero et al., 2020).

Regarding scale of analysis, the prevalence of *P. bocagei* seems to influence modelling results, as this species' generalist habits and resilience to fragmentation (Galán, 2015) may result in a stronger relationship with coarser scales. Particularly at this scale, current vegetation cover is highlighted as the most relevant factor influencing reptile species richness in Porto, aligning with other studies (e.g., De Solan et al., 2019; Vignoli et al., 2009). The results also suggest that reptiles benefit from both wooded and herbaceous habitats, which provide diverse ecological conditions necessary for foraging, basking, predator avoidance, egg-laying, and overwintering (Pulsford et al., 2018). In Porto, some locations balance tree/shrub cover and herbaceous cover, apparently benefiting reptiles (e.g., Quinta de Bonjóia, Nova Sintra Park, Pasteleira Park, Asprela area).

Although current land cover seems fundamental for reptile distribution, past land cover seems to also play an important role: higher species richness occurs in areas extensively vegetated both in 1979 and 1947, even if that vegetation was substantially reduced recently (e.g., in Amial, Areosa, and Senhora de Campanhã). This can indicate a phenomenon of extinction debt (Figueiredo et al., 2019; Kuussaari et al., 2009), where species temporarily persist in smaller patches following habitat loss and fragmentation. The response to artificial areas also seems dependent on a time scale, as areas urbanised for over 40 years displayed lower reptile occurrence and richness, while the recently built-up areas do not seem to have a significant impact. Due to this delayed response, population decline could be reverted with improved habitat quality and strengthened connectivity with source populations.

The predicted species richness distribution shows an arc-shaped pattern of reptile occurrence in the city's periphery, with reptiles seemingly excluded from the city centre. The dominance of *P. bocagei* in Porto seems to influence the predicted spatial distributions of reptiles. Despite models pointing to the importance of past vegetation cover, spatial predictions of the average model failed to capture reptile persistence in

smaller habitat patches associated with older vegetation patches. Most of these (e.g., in Amial, Areosa, and Senhora de Campanhã) have recently experienced habitat loss and fragmentation, retaining only a fraction of the historic habitat cover and composition. This raises concern about future local extinction of the dwindling *P. bocagei* populations at these sites, as occurred recently in other locations in Porto (authors' unpublished data).

### *4.5.3. Species richness of amphibians*

The low species richness and low rate of occurrence of amphibians greatly conditioned the performance of the modelling framework (most models have $\Delta_i$ >6), but our results can help unveil the history of the amphibian populations of Porto.

As expected, the presence of water elements seems to be a core determinant of the occurrence of amphibian species, but other factors must be considered. Almost half of the sampled squares (19 in 43 sites) had water elements, but only six were occupied by amphibians, which could indicate unsuitable aquatic habitats, poor upland habitat quality or availability, or isolation. Many water elements in Porto's green spaces, such as tanks and fountains, are small, artificialized, have steep margins or walls, lack aquatic vegetation, and some are populated by fish, being detrimental for amphibians (Cruz et al., 2015; Fuyuki et al., 2014; Hamer et al., 2011; Parris, 2006).

Amphibian species in Porto seem to favour areas with older vegetation patches, especially those with arboreal cover in 1979, showing a positive effect similar to Piha et al. (2007) and Busby et al. (2022) for historic forests. Older green spaces, like the Botanical Garden, Virtudes Garden, Nova Sintra Park, or Covelo Park, still retain some small amphibian populations, possibly due to maintaining a high habitat heterogeneity and quality, a legacy from their past as recreational farms in the 19$^{th}$ century. Other older green spaces (e.g., Arca d'Água Garden, Passeio Alegre Garden, Carregal Garden), despite having a similar vegetation structure and composition, do not support amphibians as they lack suitable water features. Similarly, the modelling results suggest a negative relation between amphibians and recent vegetation patches, which present a lesser developed vegetation structure and/or no adequate aquatic habitats (e.g., José Roquette Garden, Sophia's Garden). These results may, therefore, arise from the combination of the predominance of adequate aquatic habitats and complex vegetation structures only in older parks with the limited abilities of this group for dispersal and colonization of newer green spaces (Busby et al., 2022).

The models also seem to point to a negative association between amphibians and historical herbaceous cover (1979 and 1947), possibly indicating a time-lagged response to former agricultural areas (Piha et al., 2007). On the other hand, the areas with herbaceous vegetation in 1979 and 1947, were prioritized for urbanisation, which could reflect a negative response to built-up or impervious cover, as reported by several authors (e.g., Guderyahn et al., 2016; Villaseñor et al., 2017).

Despite the low model performance, the predicted spatial pattern of amphibian occurrence seems to be relatively accurate, but fails to predict values above one species, as observed in Botanical Garden and Virtudes Garden (3 species in each site). Overall, amphibians seem to be concentrated in very few isolated locations; besides the sampled sites, the modelling results seem to correctly predict the occurrence of amphibian species in other locations, such as the City Park, Serralves Park, Prelada Park, Palácio de Cristal Gardens, São Roque Park, or Oriental Park, as demonstrated by previous studies (authors' unpublished data; Pereira, 2011; Ribeiro, 2011). This severely discontinuous distribution may indicate a delayed response to habitat loss and fragmentation, where amphibians are not able to cross the inhospitable urban matrix and become "trapped" in extremely reduced habitat patches. The modelling results appear to support the sedentary profile of amphibians and emphasize the importance of small habitat patches (even if isolated), as fine-scale models outperformed coarse-scale models (Öckinger et al., 2009).

### *4.5.4. Implications for urban planning and urban biodiversity conservation*

At first glance, the future does not look promising for the preservation of urban biodiversity in Porto, as two-thirds of the city is covered by built-up and impervious surfaces (Guilherme et al., 2022). However, vertebrate diversity in Porto remains noteworthy, with 70% of regional amphibian species, 54% of regional reptile species, and 23% of regional bird species (Farinha-Marques et al., 2023; Guilherme et al., 2015).

All studied fauna groups seem to respond to past land cover or land cover legacy – the oldest vegetation patches tend to host more species, while older urban areas are less biodiverse. The more biodiverse green spaces are 19$^{th}$-century parks and gardens (e.g., Passeio Alegre Garden, Palácio de Cristal Gardens) and recent public parks that originated from recreational farms, agricultural and forest land (e.g., City Park, Serralves Park, Covelo Park, Oriental Park). Their status as public green spaces has led to the preservation, protection and promotion of habitat, flora, and fauna diversity; the same

does not apply to the substantial proportion of undeveloped land that has, nonetheless, sustained its vegetation cover for over 72 years. Older and stable habitat patches foster a complex vegetation structure and diverse habitat niches, which enhances their biodiversity (Janssen et al., 2017; Nordén et al., 2014), especially for specialist, long-lived, and/or dispersal-limited species (Lira et al., 2019). As such, to maintain a higher species richness at the city level, it is essential to preserve the parks and gardens, as well as the undeveloped land, to the possible extent – the conservation of habitats in Ervilheira/Nevogilde, Prelada/Viso, Asprela, Contumil/Currais, Rio Tinto and Rio Torto seems to be particularly imperative, due to their city-wide relevance and the pressure to urbanise them (Buonincontri et al., 2023; Guilherme et al., 2024). If, or when, these spaces are urbanised, it is fundamental to preserve large patches of continuous vegetation, that could act as habitat and dispersion corridors. To complement habitat preservation and counteract the habitat loss at the city scale, it is also important to regenerate or create new habitats near older vegetation patches, as it facilitates dispersal and colonization of new green spaces, vital for species with limited dispersion abilities. Birds, being highly mobile, seem to respond positively to recent vegetation cover, unlike less mobile species such as amphibians and reptiles that face more challenges when transversing the urban matrix.

Besides preserving older habitats and creating new ones, the options for the design, composition, and maintenance, of both existing and future green spaces, should be conducive to high biodiversity levels. Green spaces should incorporate a combination of woodlands, clearings, and multiple vertical layers of vegetation, along with specific microhabitat elements in strategic locations, such as water elements for amphibians, refuges for reptiles, nest boxes for birds, plant species associated with fauna species, etc. This could be decisive for the conservation of rare or specialist species, as well as common species struggling in dense urban environments (Jokimäki et al., 2018).

Amphibians can be considered the most vulnerable vertebrate group in Porto, for which conservation measures are most pressing. They are highly susceptible to fragmentation, but are able to maintain precarious populations in small habitat patches if the habitat requirements are met (Raquel Ribeiro, Sillero, et al., 2009). The preservation of the few parks and gardens where amphibians occur (e.g., City Park, Serralves Park, Pasteleira Park, Botanical Garden, Palácio de Cristal Gardens, Virtudes Garden, Prelada Park, Covelo Park, S. Roque Park, Nova Sintra Park, and Oriental Park) would also have an “umbrella effect” on other vertebrates. In other green areas with adequate upland habitats, but where amphibians currently do not occur (e.g., Palácio de Cristal Gardens),

we recommend implementing adequate water features suitable for reproduction or improving the existing ones. These measures should be complemented with the creation of strategic green corridors, especially in the northern peripherical arc, along the bank of the Douro River, and in the western section of the city. This would facilitate amphibian dispersal through the urban fabric, promoting the colonization of new areas and maintaining a greater genetic diversity in existing populations (Velo-Antón et al., 2021).

Reptiles are also rather scarce in Porto, but the most common species is quite resistant to fragmentation and able to persist in urbanised areas with reduced vegetation. Other species face challenges finding suitable habitats and are sensitive to fragmentation. To promote reptile presence, recommended measures involve guaranteeing diverse microhabitats in remaining vegetated areas (Croci et al., 2008), focusing on places for refuge or shelter for target species. Given reptiles' reduced dispersal, it is crucial to reinforce the connectivity between green spaces and to create new green spaces to function as stepping stones.

Birds are the most successful group of vertebrates in Porto, with even early urbanised areas presenting interesting levels of species richness. However, this diversity often stems from commensal, opportunistic and/or exotic species, particularly in the city centre. To balance this situation, the presence of specialist and rare species should be encouraged by diversifying habitat niches in strategic locations, as current green areas have a simplified vegetation structure and composition, only benefiting a restricted number of species. Recommendations include installing nest boxes for cavity-nesting birds and emphasizing shrub and herbaceous layers to complement trees. Since birds seem to positively respond to recent habitat transformation and can overcome isolation caused by the urban matrix, we recommend the multiplication and enlargement of green spaces, mainly towards the biologically impoverished city centre. These measures could deliver quick results even in scenarios of lower physical connectivity (Evans et al., 2009).

### *4.5.5. Limitation and future research*

For this study, we intended to understand the response of different fauna groups to the land cover evolution in Porto, in the close historical past for which there is remote sensing data. Although this was not possible due to limited resources and lack of available data, we recommend using shorter time intervals to better capture the fast-paced dynamics of urban areas and the biodiversity response to these dynamics. Other limitation was the reduced number of records of species occurrences, either within the study area or in the

surroundings. If sufficient records were available, model of species occupancies could be produced and, subsequently, potential species richness could be estimated (Raquel Ribeiro, Santos, et al., 2009). Lacking this information, species richness had to be calculated from current individual data on each species. While already expected, due to the biological impoverishment of urban areas that is detrimental to species abundance and diversity, the excess of "zeros" had repercussions in the statistical analysis. Primarily, as indicated by the values of AIC and $\Delta_i$, it affected the robustness of most of the models. Despite the low statistical support, the modelling results and the spatial predictions reveal interesting tendencies and patterns that line up with our previous knowledge about vertebrate species distribution in the city of Porto. Additionally, we were not able to test complex interactions among variables, as they can be challenging to implement in a multimodel inference framework. The evaluation of interactions is limited to variables present in a specific model and interactions might occur between variables not shared within the same model. As each model relates to a different hypothesis, this could lead to confounding effects when testing among competing hypotheses. We argue that, while not strictly required for testing our primary hypotheses, interactions could enhance the fit of certain models and help support some of them; this should be a research focus for the near future.

We acknowledge that for decision-making on the preservation and regeneration of habitats at the city scale, as well as their design and management at the local scale, information on site species richness may not be sufficient. For future research on the influence of land use legacy on urban biodiversity, a functional ecology perspective could be valuable to provide a more accurate portrayal of the relationship. It would be beneficial to know the species composition of communities, the species diversity at larger scales, and identify priority species for conservation. As a general rule, the most sensitive species, those with greater ecological specificities, or those with a more restricted distribution, should be prioritized.

## 4.6. Conclusions and recommendations

In conclusion, our research of vertebrate biodiversity in the city of Porto has provided valuable insights into the complex interplay between land cover evolution and the species richness distribution of birds, reptiles, and amphibians. Birds, with their higher diversity, mobility, and adaptability, are able to thrive in a broader range of habitats, including new green spaces and areas with recent vegetation cover, which underscores

the importance of urban planning that prioritizes the preservation and regeneration of older habitats, as well as the creation of new ones in previously urbanised areas. This brings hope to the promotion of biodiversity in the city centre, which is currently biologically impoverished, as birds present a high probability to colonize new habitat patches, even with low physical connectivity, if the right local habitat requirements are met. Since the bird species pool in Porto is rather diverse, we recommend the provision of diverse vegetation layers and nesting structures.

Amphibians and reptiles, on the other hand, face more challenges in urban environments, with only a few species able to adapt to the heavily urbanised areas of Porto. Reptiles have been able to persist mostly in the peripheral arc, where green spaces are more abundant. Our study highlights the need for maintaining a diverse matrix of vegetation and habitats, ensuring the presence of suitable microhabitats, and strengthening connectivity between urban green spaces, as well as nearby semi-natural habitats, to support reptile populations. Amphibians, with their limited mobility, are particularly vulnerable to habitat fragmentation, and their occurrence in Porto is essentially concentrated in older parks and gardens. To safeguard both groups, it is crucial to preserve and enhance the quality of green spaces, implement water features suitable for amphibians, and establish strategic green corridors to facilitate dispersal.

While urbanisation continues to expand, efforts must be made to strike a balance between urban development and biodiversity preservation, which should be considered in the multiple stages of urban planning, design, and management. This involves not only conserving older habitats, but also creating new ones, even in areas where urbanisation is to occur, fostering diverse vegetation and microhabitats, and prioritizing the most sensitive and specialist species. By implementing these recommendations, Porto can work towards preserving and improving its biodiversity and ensuring a sustainable coexistence between its human and natural inhabitants. This study serves as a valuable resource for decision-makers, urban planners, and conservationists in their efforts to create a more ecologically resilient and biodiverse city.

# 4.7. Supplementary material

## *4.7.1. Observed data*

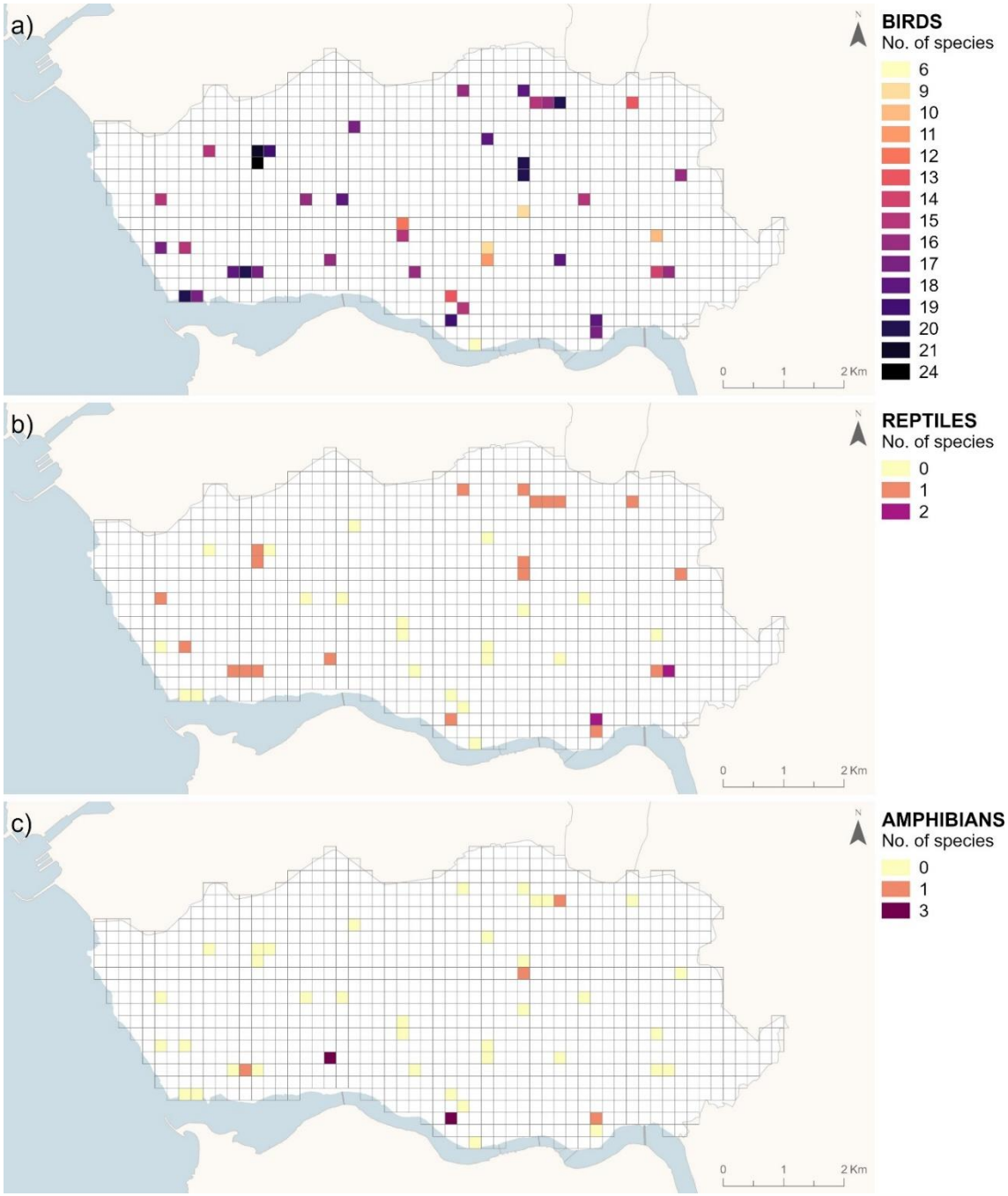



**Figure 4.4.** Observed species richness of birds (a), reptiles (b), and amphibians (c), obtained during fieldwork in 2019 and 2021.

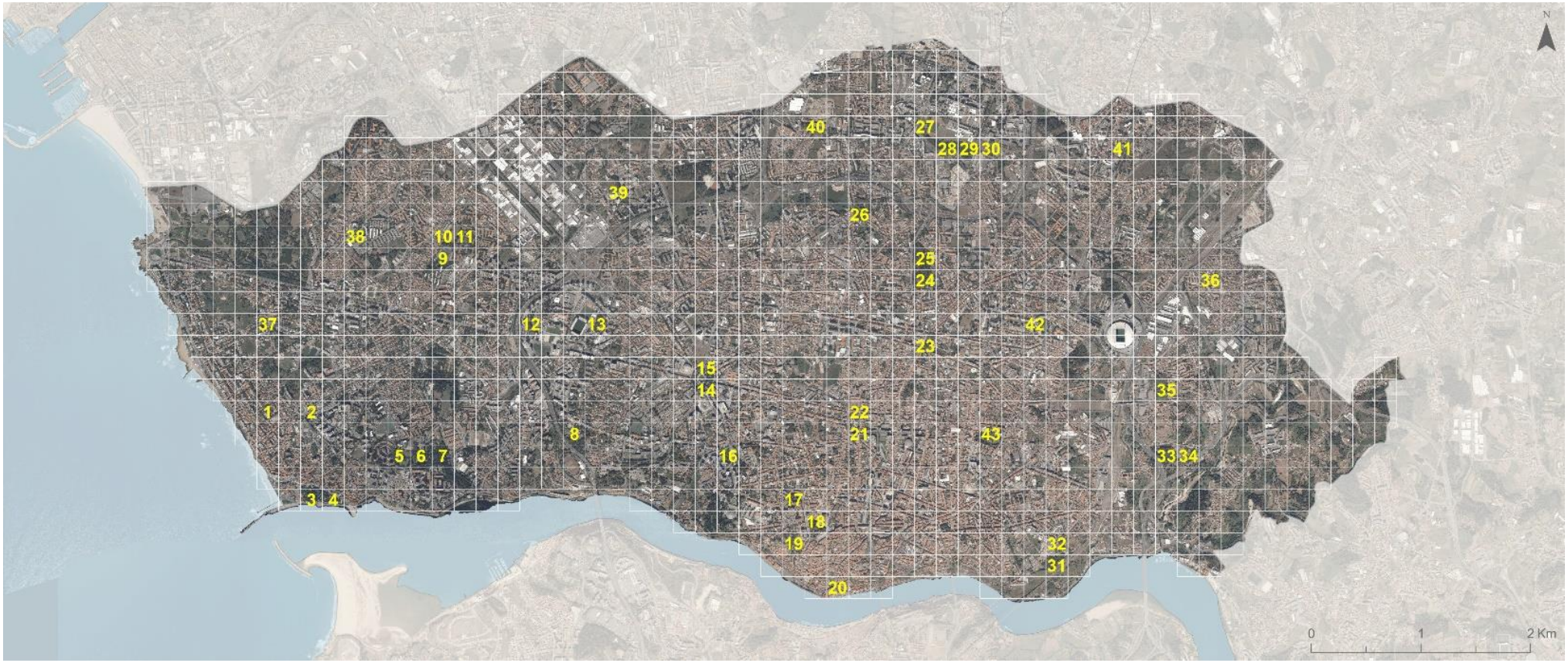



**Figure 4.5.** Sampling sites identified by a numeric code.

**Table 4.6.** Species recorded in the sampling sites, during fieldwork in 2019 and 2021 (check location in Figure 4.5).

| SITES | 20 | 22 | 23 | 35 | 21 | 15 | 17 | 41 | 14 | 18 | 38 | 42 | 33 | 12 | 16 | 2 | 28 | 37 | 1 | 4 | 39 | 29 | 36 | 40 | 13 | 43 | 26 | 7 | 31 | 34 | 11 | 5 | 27 | 3 | 8 | 25 | 32 | 10 | 6 | 24 | 30 | 19 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Bird species richness** | **6** | **9** | **9** | **10** | **11** | **12** | **13** | **13** | **15** | **15** | **15** | **15** | **14** | **16** | **16** | **15** | **15** | **15** | **17** | **17** | **17** | **16** | **16** | **16** | **18** | **18** | **18** | **17** | **17** | **16** | **19** | **18** | **18** | **20** | **16** | **20** | **18** | **21** | **20** | **20** | **20** | **19** | **24** |
| *Aegithalos caudatus* | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | | | | | | | | | | | | | |
| *Agapornis* sp. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • |
| *Alopochen aegyptiacus* | | | | | | | • | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | | | • | | | |
| *Anas platyrhynchos* | | | | | | | • | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | | | • | | | |
| *Carduelis carduelis* | | | | | | | | | • | | | | | | | | • | | | | | | • | | | • | | | | | | | | | | | • | | | | • | | |
| *Carduelis chloris* | | • | | | | • | | • | • | • | • | • | | • | • | | • | | • | | • | | • | • | | • | • | • | | • | | | • | • | • | • | • | • | • | • | • | • |
| *Certhia brachydactyla* | | | | • | | | • | | | • | | | | • | | | | | | • | | | | | • | | • | • | • | • | • | • | | • | • | • | • | | • | • | | • |
| *Cisticola juncidis* | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | | | | | • | | | | | |
| *Columba livia* | • | • | • | • | • | • | • | • | • | • | • | • | | • | • | • | | • | • | • | • | | • | • | • | • | • | • | | • | • | • | • | • | • | • | • | • | • | • | • | • | • |
| *Columba palumbus* | | | | • | • | • | • | | • | • | | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • |
| *Cyanopica cyanus* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | |
| *Delichon urbicum* | | | | | | | | • | | | | | | | | | | | | | • | | | • | | | | | | | | | • | | | | | | | | • | | |
| *Erithacus rubecula* | | | | | | • | | | • | | • | • | • | • | • | • | • | • | | • | | • | | | • | | • | • | • | • | • | • | • | • | • | • | | | • | • | • | • | • |
| *Estrilda astrid* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | |
| *Fringilla coelebs* | | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | | | | | | | | | | | |
| *Gallinula chloropus* | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | | | | | | | | | | | | |
| *Garrulus glandarius* | | | | | | | | • | | | | | • | | | | | • | | | | • | | | • | • | | | • | • | • | • | | | | • | • | • | • | • | • | | • |
| *Hirundo rustica* | | | | | | | | | | | • | | | | | | | | • | • | • | | | | | • | | | | | • | • | | | | | | • | | | | | |
| *Larus michahellis* | • | • | • | • | • | • | • | • | • | • | • | • | | | • | • | | • | • | • | | | | | • | • | • | | | | • | | • | | • | • | • | • | • | • | • | • |
| *Motacilla alba* | • | • | • | • | • | • | | | • | • | • | • | | • | • | • | | | | • | • | • | • | • | • | • | | • | | | • | • | • | • | | | • | • | • | • | | • |
| *Myiopsitta monachus* | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | • | | | | | | • | | | | | | | • | | • |
| *Parus ater* | | • | • | | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • |
| *Parus caeruleus* | | | | • | | | | | | | | | • | | | | | | • | | | | | | | | | | • | | | | | • | • | • | • | | | • | | |
| *Parus major* | | | • | | • | • | | | • | | | • | • | • | • | • | • | • | | | • | • | | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • |
| *Passer domesticus* | • | • | • | • | • | • | | • | • | • | • | • | | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | | | • | | • | • | | • | • | • | | • | • | • |
| *Phoenicurus ochruros* | | | | | | | | | | • | | | • | | | | | • | • | | • | | | | | • | | | • | | | | | | | | • | | | | • | • | • |

**Table 4.6.** (continued)

| SITES | 20 | 22 | 23 | 35 | 21 | 15 | 17 | 41 | 14 | 18 | 38 | 42 | 33 | 12 | 16 | 2 | 28 | 37 | 1 | 4 | 39 | 29 | 36 | 40 | 13 | 43 | 26 | 7 | 31 | 34 | 11 | 5 | 27 | 3 | 8 | 25 | 32 | 10 | 6 | 24 | 30 | 19 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pica pica* | | | | • | | | • | • | | | • | | | • | | • | • | • | • | • | • | • | | • | • | | • | • | | • | • | • | • | • | • | | | | | • | • | • |
| *Picus viridis* | | | | | | | | | | | | • | | | | | | | | | | | | | | | | | • | • | • | | | | • | | | | • | | | • | • |
| *Prunella modullaris* | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | | | | | | | | | | | | | |
| *Psittacula krameri* | | | | | | | | | | | | | | | | | | | • | • | | | | • | | | | | | | | | | • | | | | | | | | • | | | |
| *Regulus ignicapillus* | | | | | | | • | • | | • | • | • | • | | | | • | | | | | | • | | • | • | | | • | | | | | • | • | • | • | • | • | • | | • | • |
| *Serinus serinus* | • | | | • | • | | • | | | • | • | • | | • | • | • | • | • | • | • | • | | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • |
| *Streptopelia decaocto* | | • | • | | • | | • | • | • | • | • | • | | • | • | • | | • | • | • | | • | • | • | • | • | • | • | | • | | • | • | • | • | • | • | • | • | • | • | • |
| *Streptopelia turtur* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | |
| *Sturnus unicolor* | | • | | | | • | | | • | • | | | • | | • | • | | | • | | | | • | | • | • | • | • | • | | • | • | | • | • | • | • | • | • | | • | • | • |
| *Sylvia atricapilla* | | | | | • | • | | • | • | | • | | • | • | • | • | • | • | • | • | • | • | • | • | • | | | | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • |
| *Sylvia undata* | | | | | | | | | | | | | • | | | | • | | | | | • | | | | | | | | | | | • | | | | | | | | | | |
| *Troglodytes troglodytes* | | | • | | | | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • |
| *Turdus merula* | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • | • |
| *Turdus philomelos* | | | | | | | | | | | | | • | • | • | | • | | | | • | • | | | | | • | • | • | • | • | • | | | • | • | | | • | • | | | • |
| unidentified Psittacidae | | | | | | | | | | | | | | | | | | | | | | | • | | | | | • | | | | | | | | | | | | | | | | |
| ***Reptile species richness*** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **1** | **0** | **0** | **0** | **0** | **1** | **0** | **0** | **1** | **1** | **1** | **0** | **0** | **0** | **1** | **1** | **1** | **0** | **0** | **0** | **1** | **1** | **2** | **0** | **1** | **1** | **0** | **1** | **1** | **2** | **1** | **1** | **1** | **1** | **1** | **1** |
| *Coronella girondica* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | | | | | | |
| *Podarcis bocagei* | | | | | | | | • | | | | | • | | | • | • | • | | | | • | • | • | | | | • | | • | | • | • | | • | • | | • | • | • | • | | • |
| *Podarcis lusitanicus* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | • | | | | • | | |
| *Psammodromus algirus* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | | |
| ***Amphibian species richness*** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **3** | **0** | **1** | **0** | **1** | **1** | **1** | **3** | **0** |
| *Alytes obstetricans* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | • | |
| *Lissotriton boscai* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | |
| *Pelophylax perezi* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | • | • | • | • | |
| *Salamandra salamandra* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | |
| *Triturus marmoratus* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | • | | | | | | | | |
| ***Combined species richness*** | **6** | **9** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **15** | **15** | **15** | **15** | **16** | **16** | **16** | **16** | **16** | **17** | **17** | **17** | **17** | **17** | **17** | **18** | **18** | **18** | **18** | **18** | **18** | **19** | **19** | **19** | **20** | **20** | **21** | **21** | **22** | **22** | **22** | **22** | **23** | **25** |

### *4.7.2. Complete modelling results*

Complete results of information-theoretic-based model selection and multimodel inference, regarding the number of parameters (*K*), AIC difference ($\Delta_i$ ), Akaike weights ($w_i$), adjusted $R^2$, predictors, and their effect on species richness.

**Table 4.7.** Complete results of information-theoretic-based model selection and multimodel inference for bird species richness, showing the number of parameters (*K*), AIC difference ($\Delta_i$ ), Akaike weights ($w_i$), adjusted $R^2$, predictors, and their effect on bird species richness, for the 33 considered models.

| Model | *K* | $\Delta_i$ | $w_i$ | adj. $R^2$ | predictors | effect |
|---|---|---|---|---|---|---|
| M19: Artificial cover in 1947 (fine scale) | 3 | 0 | 0.152082 | 0.235324 | ABE1947F | negative |
| M7: Artificial cover in 2019 (fine scale) | 3 | 0.039688 | 0.149094 | 0.234169 | ABE2019F | negative |
| M5: Vegetation cover in 2019 (fine scale) | 3 | 0.619803 | 0.111555 | 0.217284 | Veg2019F | positive |
| M18: Vegetation cover in 1947 (coarse scale) | 3 | 1.031569 | 0.090798 | 0.205298 | Veg1947C | positive |
| M17: Vegetation cover in 1947 (fine scale) | 3 | 1.055675 | 0.08971 | 0.204597 | Veg1947F | positive |
| M31: Vegetation cover change (fine scale) | 6 | 1.271058 | 0.080551 | 0.36497 | Veg72yF<br>VegDisturbF<br>VegGainF<br>VegLossF | positive<br>positive<br>positive<br>positive |
| M20: Artificial cover in 1947 (coarse scale) | 3 | 2.41604 | 0.04544 | 0.165001 | ABE1974C | negative |
| M3: Type of vegetation cover in 2019 (fine scale) | 4 | 2.870273 | 0.036208 | 0.199652 | TRS2019F<br>HER2019F | positive<br>positive |
| M16: Type of vegetation cover in 1947 (coarse scale) | 4 | 2.911869 | 0.035463 | 0.198411 | TRS1947C<br>HER1947C | positive<br>positive |
| M15: Type of vegetation cover in 1947 (fine scale) | 4 | 3.088168 | 0.032471 | 0.193152 | TRS1947F<br>HER1947F | positive<br>positive |
| M4: Type of vegetation cover in 2019 (coarse scale) | 4 | 3.7773746 | 0.0230055 | 0.1725896 | TRS2019C<br>HER2019C | positive<br>negative |
| M6: Vegetation cover in 2019 (coarse scale) | 3 | 3.8653627 | 0.0220153 | 0.1228163 | Veg2019C | positive |
| M13: Artificial cover in 1979 (fine scale) | 3 | 4.1923919 | 0.0186944 | 0.1132976 | ABE1979F | negative |
| M14: Artificial cover in 1979 (coarse scale) | 3 | 4.6660573 | 0.0147522 | 0.0995108 | ABE1979C | negative |
| M22: Age of tree and shrub cover (coarse scale) | 5 | 4.89909 | 0.0131297 | 0.1916283 | TRS72yC<br>TRS4071yC<br>TRS039C | positive<br>negative<br>positive |
| M11: Vegetation cover in 1979 (fine scale) | 3 | 5.0817853 | 0.0119834 | 0.0874104 | Veg1979F | positive |
| M12: Vegetation cover in 1979 (coarse scale) | 3 | 5.640981 | 0.0090605 | 0.0711341 | Veg1979C | positive |
| M8: Artificial cover in 2019 (coarse scale) | 3 | 5.6710127 | 0.0089255 | 0.07026 | ABE2019C | negative |

**Table 4.7.** (continued)

| Model | *K* | $\Delta_i$ | $w_i$ | adj. $R^2$ | predictors | effect |
|---|---|---|---|---|---|---|
| M25: Age of vegetation cover (fine scale) | 5 | 6.2430119 | 0.0067054 | 0.1505053 | Veg72yF<br>Veg4071yF<br>Veg039yF | positive<br>positive<br>negative |
| M2: Water (coarse scale) | 3 | 6.2771698 | 0.0065919 | 0.0526168 | WaterC | positive |
| M32: Vegetation cover change (coarse scale) | 6 | 6.4312301 | 0.0061031 | 0.2029171 | Veg72yC<br>VegDisturbC<br>VegGainC<br>VegLossC | positive<br>positive<br>positive<br>negative |
| M26: Age of vegetation cover (coarse scale) | 5 | 6.4804721 | 0.0059547 | 0.1432392 | Veg72yC<br>Veg4071yC<br>Veg039yC | positive<br>positive<br>negative |
| M27: Tree and shrub cover change (fine scale) | 6 | 6.5207169 | 0.0058361 | 0.2001068 | TRS72yF<br>TRSDisturbF<br>TRSGainF<br>TRSLossF | positive<br>positive<br>positive<br>negative |
| M9: Type of vegetation cover in 1979 (fine scale) | 4 | 7.3971539 | 0.0037654 | 0.0645961 | TRS1979F<br>HER1979F | positive<br>positive |
| M28: Tree and shrub cover change (coarse scale) | 6 | 7.5269335 | 0.0035288 | 0.1685071 | TRS72yC<br>TRSDisturbC<br>TRSGainC<br>TRSLossC | positive<br>positive<br>positive<br>negative |
| M1: Water (fine scale) | 3 | 7.5599766 | 0.003471 | 0.0152786 | WaterF | positive |
| M23: Age of herbaceous cover (fine scale) | 5 | 7.724796 | 0.0031964 | 0.1051638 | HER72yF<br>HER4071yF<br>HER039yF | positive<br>positive<br>negative |
| M10: Type of vegetation cover in 1979 (coarse scale) | 4 | 7.7595056 | 0.0031414 | 0.0537856 | TRS1979C<br>HER1979C | positive<br>positive |
| M21: Age of tree and shrub cover (fine scale) | 5 | 8.1391936 | 0.0025982 | 0.0924835 | TRS72yF<br>TRS4071yF<br>TRS039F | positive<br>positive<br>positive |
| M33: Null model | 3 | 8.9000093 | 0.0017761 | -0.023725 | - | - |
| M24: Age of herbaceous cover (coarse scale) | 5 | 9.1507647 | 0.0015668 | 0.0615302 | HER72yC<br>HER4071yC<br>HER039yC | positive<br>positive<br>negative |
| M30: Herbaceous cover change (coarse scale) | 5 | 11.24335 | 0.0005503 | -0.002501 | HER72yC<br>HERDisturbC<br>HERGainC | positive<br>positive<br>negative |
| M29: Herbaceous cover change (fine scale) | 6 | 12.615976 | 0.000277 | 0.0086882 | HER72yF<br>HERDisturbF<br>HERGainF<br>HERLossF | positive<br>positive<br>negative<br>positive |

**Table 4.8.** Complete results of information-theoretic-based model selection and multimodel inference for reptile species richness, showing the number of parameters (*K*), AIC difference ($\Delta_i$ ), Akaike weights ($w_i$), adjusted $R^2$, predictors, and their effect on reptile species richness, for the 33 considered models.

| Model | *K* | $\Delta_i$ | $w_i$ | adj. $R^2$ | predictors | effect |
|---|---|---|---|---|---|---|
| M6: Vegetation cover in 2019 (coarse scale) | 3 | 0 | 0.308051 | 0.328195 | Veg2019C | positive |
| M4: Type of vegetation cover in 2019 (coarse scale) | 4 | 2.298104 | 0.097633 | 0.31194 | TRS2019C<br>HER2019C | positive<br>positive |
| M14: Artificial cover in 1979 (coarse scale) | 3 | 2.565197 | 0.085427 | 0.249839 | ABE1979C | negative |
| M11: Vegetation cover in 1979 (fine scale) | 3 | 2.754337 | 0.077719 | 0.244061 | Veg1979F | positive |
| M20: Artificial cover in 1947 (coarse scale) | 3 | 3.46306 | 0.054529 | 0.222413 | ABE1947C | negative |
| M17: Vegetation cover in 1947 (fine scale) | 3 | 3.818592 | 0.045648 | 0.211553 | Veg1947F | positive |
| M12: Vegetation cover in 1979 (coarse scale) | 3 | 4.239417 | 0.036987 | 0.198698 | Veg1979C | positive |
| M19: Artificial cover in 1947 (fine scale) | 3 | 4.255886 | 0.036683 | 0.198195 | ABE1947F | negative |
| M13: Artificial cover in 1979 (fine scale) | 3 | 4.470407 | 0.032952 | 0.191642 | ABE1979F | negative |
| M5: Vegetation cover in 2019 (fine scale) | 3 | 4.547676 | 0.031704 | 0.189282 | Veg2019F | positive |
| M8: Artificial cover in 2019 (coarse scale) | 3 | 4.7832247 | 0.0281812 | 0.1820871 | ABE2019C | negative |
| M9: Type of vegetation cover in 1979 (fine scale) | 4 | 4.8224512 | 0.0276338 | 0.2329045 | TRS1979F<br>HER1979F | positive<br>positive |
| M10: Type of vegetation cover in 1979 (coarse scale) | 4 | 4.9254982 | 0.0262461 | 0.2296782 | TRS1979C<br>HER1979C | positive<br>positive |
| M3: Type of vegetation cover in 2019 (fine scale) | 4 | 5.5704709 | 0.0190112 | 0.2094844 | TRS2019F<br>HER2019F | positive<br>positive |
| M22: Age of tree and shrub cover (coarse scale) | 5 | 5.8410166 | 0.0166059 | 0.2587925 | TRS72yC<br>TRS4071yC<br>TRS039yC | positive<br>positive<br>positive |
| M7: Artificial cover in 2019 (fine scale) | 3 | 6.0361706 | 0.0150621 | 0.1438148 | ABE2019F | negative |
| M15: Type of vegetation cover in 1947 (fine scale) | 4 | 6.0705818 | 0.0148051 | 0.1938262 | TRS1947F<br>HER1947F | positive<br>positive |
| M18: Vegetation cover in 1947 (coarse scale) | 3 | 6.3533536 | 0.0128532 | 0.1341262 | Veg1947C | positive |
| M31: Vegetation cover change (fine scale) | 6 | 7.9091341 | 0.0059044 | 0.2557944 | Veg72yF<br>VegDisturbF<br>VegGainF<br>VegLossF | positive<br>positive<br>positive<br>positive |
| M16: Type of vegetation cover in 1947 (coarse scale) | 4 | 8.2817431 | 0.0049008 | 0.124596 | TRS1947C<br>HER1947C | positive<br>positive |

**Table 4.8.** (continued)

| Model | *K* | $\Delta_i$ | $w_i$ | adj. $R^2$ | predictors | effect |
|---|---|---|---|---|---|---|
| M28: Tree and shrub cover change (coarse scale) | 6 | 9.2056261 | 0.0030878 | 0.2130655 | TRS72yC<br>TRSDisturbC<br>TRSGainC<br>TRSLossC | positive<br>negative<br>positive<br>negative |
| M2: Water (coarse scale) | 3 | 9.2873374 | 0.0029642 | 0.0445053 | WaterC | positive |
| M25: Age of vegetation cover (fine scale) | 5 | 9.3349888 | 0.0028944 | 0.1465931 | Veg72yF<br>Veg4071yF<br>Veg039yF | positive<br>positive<br>negative |
| M26: Age of vegetation cover (coarse scale) | 5 | 9.5295085 | 0.0026261 | 0.1403466 | Veg72yC<br>Veg4071yC<br>Veg039yC | positive<br>positive<br>negative |
| M30: Herbaceous cover change (coarse scale) | 5 | 9.7300927 | 0.0023755 | 0.1339054 | HER72yC<br>HERDisturbC<br>HERGainC | positive<br>positive<br>positive |
| M33: Null model | 3 | 10.165762 | 0.0019105 | 0.0176731 | - | - |
| M24: Age of herbaceous cover (coarse scale) | 5 | 11.241284 | 0.0011159 | 0.0853777 | HER72yC<br>HER4071yC<br>HER039yC | positive<br>positive<br>positive |
| M21: Age of tree and shrub cover (fine scale) | 5 | 11.517128 | 0.0009721 | 0.0765197 | TRS72yF<br>TRS4071yF<br>TRS039yF | positive<br>positive<br>positive |
| M1: Water (fine scale) | 3 | 11.54245 | 0.0009599 | -0.024379 | WaterF | negative |
| M23: Age of herbaceous cover (fine scale) | 5 | 11.62492 | 0.0009211 | 0.0730582 | HER72yF<br>HER4071yF<br>HER039yF | positive<br>positive<br>negative |
| M32: Vegetation cover change (coarse scale) | 6 | 11.8674 | 0.0008159 | 0.1253406 | Veg72yC<br>VegDisturbC<br>VegGainC<br>VegLossC | positive<br>positive<br>positive<br>positive |
| M27: Tree and shrub cover change (fine scale) | 6 | 12.915026 | 0.0004832 | 0.0908136 | TRS72yF<br>TRSDisturbF<br>TRSGainF<br>TRSLossF | positive<br>positive<br>positive<br>positive |
| M29: Herbaceous cover change (fine scale) | 6 | 13.64219 | 0.0003359 | 0.0668483 | HER72yF<br>HERDisturbF<br>HERGainF<br>HERLossF | positive<br>positive<br>positive<br>positive |

**Table 4.9.** Complete results of information-theoretic-based model selection and multimodel inference for amphibian species richness, showing the number of parameters (*K*), AIC difference ($\Delta_i$), Akaike weights ($w_i$), adjusted $R^2$, predictors, and their effect on amphibian species richness, for the 33 considered models.

| Model | *K* | $\Delta_i$ | $w_i$ | adj. $R^2$ | predictors | effect |
|---|---|---|---|---|---|---|
| M1: Water (fine scale) | 3 | 0 | 0.738084 | 0.396837 | WaterF | positive |
| M25: Age of vegetation cover (fine scale) | 5 | 3.82287 | 0.109139 | 0.389546 | Veg72yF<br>Veg4071yF<br>Veg039yF | positive<br>positive<br>negative |
| M10: Type of vegetation cover in 1979 (coarse scale) | 4 | 6.361833 | 0.030666 | 0.281446 | TRS1979C<br>HER1979C | positive<br>negative |
| M28: Tree and shrub cover change (coarse scale) | 6 | 6.819777 | 0.02439 | 0.362315 | TRS72yC<br>TRSDisturbC<br>TRSGainC<br>TRSLossC | positive<br>negative<br>positive<br>negative |
| M2: Water (coarse scale) | 3 | 7.354496 | 0.018668 | 0.218965 | WaterC | positive |
| M22: Age of tree and shrub cover (coarse scale) | 5 | 7.692374 | 0.015766 | 0.291161 | TRS72yC<br>TRS4071yC<br>TRS039yC | positive<br>positive<br>negative |
| M9: Type of vegetation cover in 1979 (fine scale) | 4 | 8.134968 | 0.012636 | 0.23749 | TRS1979F<br>HER1979F | positive<br>positive |
| M31: Vegetation cover change (fine scale) | 6 | 8.310177 | 0.011576 | 0.323423 | Veg72yF<br>VegDisturbF<br>VegGainF<br>VegLossF | positive<br>negative<br>positive<br>positive |
| M16: Type of vegetation cover in 1947 (coarse scale) | 4 | 9.115074 | 0.007741 | 0.213193 | TRS1947C<br>HER1947C | positive<br>negative |
| M21: Age of tree and shrub cover (fine scale) | 5 | 9.5757647 | 0.0061483 | 0.2432741 | TRS72yF<br>TRS4071yF<br>TRS039yF | positive<br>positive<br>negative |
| M5: Vegetation cover in 2019 (fine scale) | 3 | 9.7884687 | 0.005528 | 0.1600987 | Veg2019F | positive |
| M4: Type of vegetation cover in 2019 (coarse scale) | 4 | 10.119766 | 0.0046841 | 0.1882869 | TRS2019C<br>HER2019C | positive<br>negative |
| M32: Vegetation cover change (coarse scale) | 6 | 10.128682 | 0.0046633 | 0.2759693 | Veg72yC<br>VegDisturbC<br>VegGainC<br>VegLossC | positive<br>positive<br>positive<br>negative |
| M7: Artificial cover in 2019 (fine scale) | 3 | 10.680588 | 0.0035387 | 0.1385224 | ABE2019F | negative |
| M3: Type of vegetation cover in 2019 (fine scale) | 4 | 12.033262 | 0.0017994 | 0.1408512 | TRS2019F<br>HER2019F | positive<br>positive |
| M26: Age of vegetation cover (coarse scale) | 5 | 12.992377 | 0.0011139 | 0.1564043 | Veg72yC<br>Veg4071yC<br>Veg039yC | positive<br>positive<br>positive |
| M11: Vegetation cover in 1979 (fine scale) | 3 | 13.121566 | 0.0010442 | 0.0794863 | Veg1979F | positive |
| M13: Artificial cover in 1979 (fine scale) | 3 | 13.908928 | 0.0007044 | 0.0604436 | ABE1979F | negative |
| M27: Tree and shrub cover change (fine scale) | 6 | 15.459579 | 0.0003244 | 0.1368605 | TRS72yF<br>TRSDisturbF<br>TRSGainF<br>TRSLossF | positive<br>negative<br>positive<br>negative |

**Table 4.9.** (continued)

| Model | *K* | $\Delta_i$ | $w_i$ | adj. $R^2$ | predictors | effect |
|---|---|---|---|---|---|---|
| M6: Vegetation cover in 2019 (coarse scale) | 3 | 15.632176 | 0.0002976 | 0.0187661 | Veg2019C | positive |
| M15: Type of vegetation cover in 1947 (fine scale) | 4 | 16.417208 | 0.000201 | 0.0321728 | TRS1947F<br>HER1947F | positive<br>negative |
| M8: Artificial cover in 2019 (coarse scale) | 3 | 16.760943 | 0.0001692 | -0.008534 | ABE2019C | negative |
| M20: Artificial cover in 1947 (coarse scale) | 3 | 16.940188 | 0.0001547 | -0.012869 | ABE1947C | positive |
| M14: Artificial cover in 1979 (coarse scale) | 3 | 17.010027 | 0.0001494 | -0.014558 | ABE1979C | positive |
| M12: Vegetation cover in 1979 (coarse scale) | 3 | 17.236161 | 0.0001335 | -0.020027 | Veg1979C | positive |
| M33: Null model | 3 | 17.263694 | 0.0001316 | -0.020693 | - | - |
| M18: Vegetation cover in 1947 (coarse scale) | 3 | 17.342987 | 0.0001265 | -0.022611 | Veg1947C | positive |
| M17: Vegetation cover in 1947 (fine scale) | 3 | 17.385586 | 0.0001238 | -0.023641 | Veg1947F | positive |
| M19: Artificial cover in 1947 (fine scale) | 3 | 17.416127 | 0.000122 | -0.02438 | ABE1947F | negative |
| M23: Age of herbaceous cover (fine scale) | 5 | 17.641527 | 0.000109 | 0.0381963 | HER72yF<br>HER4071yF<br>HER039yF | negative<br>positive<br>positive |
| M29: Herbaceous cover change (fine scale) | 6 | 20.574688 | 2.51E-05 | 0.0033827 | HER72yF<br>HERDisturbF<br>HERGainF<br>HERLossF | positive<br>negative<br>positive<br>negative |
| M30: Herbaceous cover change (coarse scale) | 5 | 20.875546 | 2.16E-05 | -0.044031 | HER72yC<br>HERDisturbC<br>HERGainC | negative<br>negative<br>negative |
| M24: Age of herbaceous cover (coarse scale) | 5 | 21.007427 | 2.02E-05 | -0.047384 | HER72yC<br>HER4071yC<br>HER039yC | negative<br>negative<br>negative |

# Chapter 5.

# General discussion and conclusions

## 5.1. Thesis contributions and main findings

> *"(...) the causes of most sustainability problems are global and national, but the solutions are regional and local."*
> *(Clive A. McAlpine et al., 2013)*

We are in the midst of a biodiversity crisis (IPBES, 2019)! Urbanisation, and particularly the associated habitat loss and transformation, is one of its main drivers (McKinney, 2002; Simkin et al., 2022). In this context, the research on urban biodiversity, such as that presented in this thesis, gains relevance in the fight against the loss of biological complexity in several ways: 1) it promotes the preservation of urban biota, thus contributing to global biodiversity conservation efforts; 2) it helps to provide a better understanding of the response of organisms to land change in diverse environmental and geographic settings; 3) by operating close to human agglomerations, it contributes to raising awareness to biodiversity and environmental issues (Dearborn & Kark, 2010; Krasny et al., 2013). Considering that humans are becoming increasingly urban, future global biodiversity efforts depend on the younger generations of urban citizens, as environmental awareness is strongly influenced by a regular experience of nature, especially during childhood, which is, nowadays, mostly restricted to (peri)urban environments (Müller & Werner, 2010).

There is a growing need for urban ecological science, with a particularly important focus on the generation of "actionable knowledge" at the local scale (Jarvis & Young, 2005; McDonnell & Hahs, 2013; Wilkinson et al., 2013; Zhou et al., 2019). The evidence presented in this thesis fulfils this need, as it can be used to directly inform urban planning, design, and management decisions, not only for the city model of Porto but also for other cities in a similar context. Its temporal perspective, as well as the fine scale of approach, suits the landscape complexity and heterogeneity, and the dynamic character of urban ecosystems. The use of land cover and broad vegetation categories, as indicators of potential habitats, simplifies the quantitative analysis and facilitates communication of scientific results with decision-makers. This is especially relevant at smaller scales, as most urban interventions that translate directly into habitat loss, gain or modification occur at the site or neighbourhood scale (Brown, 2017; Opdam et al., 2013).

It should be remarked that urban biodiversity enhances the provision of ecosystem services in urban areas and can be considered an ecosystem service in itself, affecting the health and quality of life of human urbanites (Pedersen Zari, 2018). The ultimate goal of this thesis was to contribute to more sustainable, resilient, safe and healthy cities, in particular for the case of Porto, which will be synthesized in the following pages.

### *5.1.1. Land cover evolution in Porto: general perspective*

This thesis presents a spatially detailed portrait of the evolution of land cover in the city of Porto, during the second half of the 20$^{th}$ century and the beginning of the 21$^{st}$ century. Like many other cities, Porto has seen a drastic increase in the urbanisation of its territory, but it did not occur homogeneously, as different sections of the city experienced different paths and patterns of land cover evolution.

The synthesis of results and combined analysis of the spatial patterns presented in chapters 2 and 3 allowed for the definition of four main sections in the city of Porto: A) city centre, B) northern section, C) western section, and D) eastern section, exposing the diverse land cover legacies and historical socio-economic paths in different portions of the city (Figure 5.1, Box 5.1).

**Box 5.1.** Synthesis of the main trends of land cover evolution in each section of the city (see Figure 5.1).

| CITY SECTION | Main trends of land cover evolution |
|---|---|
| **A. CITY CENTRE** | Section that went through the least land cover changes in the analysed timeframe, as it was already dominated by urbanisation in 1947. Vegetation, mostly tree/shrub cover, remains in very small and isolated patches, that have been further reduced over time. |
| **B. NORTHERN SECTION** | Dominated by herbaceous vegetation, in the form of crops or pastures, from 1947 to 1979. The loss and fragmentation of vegetation patches were accelerated from 1979 to 2019, due to urban sprawl. Some significant patches of older vegetation cover still occur but are threatened by the increasing urban pressure. |
| **C. WESTERN SECTION** | Herbaceous (agricultural fields) and tree/shrub cover (forests, private gardens) were abundant in 1947. Urban growth further fragmented the remaining vegetation, but large older patches of vegetation remain relevant today. Wooded parks are valued for conservation, but the significance of herbaceous habitats in undeveloped land is overlooked. |
| **D. EASTERN SECTION** | Dominated by agricultural fields and forested land in 1947. Much of this section remains undeveloped and dominated by vegetation, but large urbanisation and transportation projects led to increased fragmentation and isolation. A significant portion of herbaceous patches have been replaced by tree/shrub cover due to the abandonment of agriculture. |

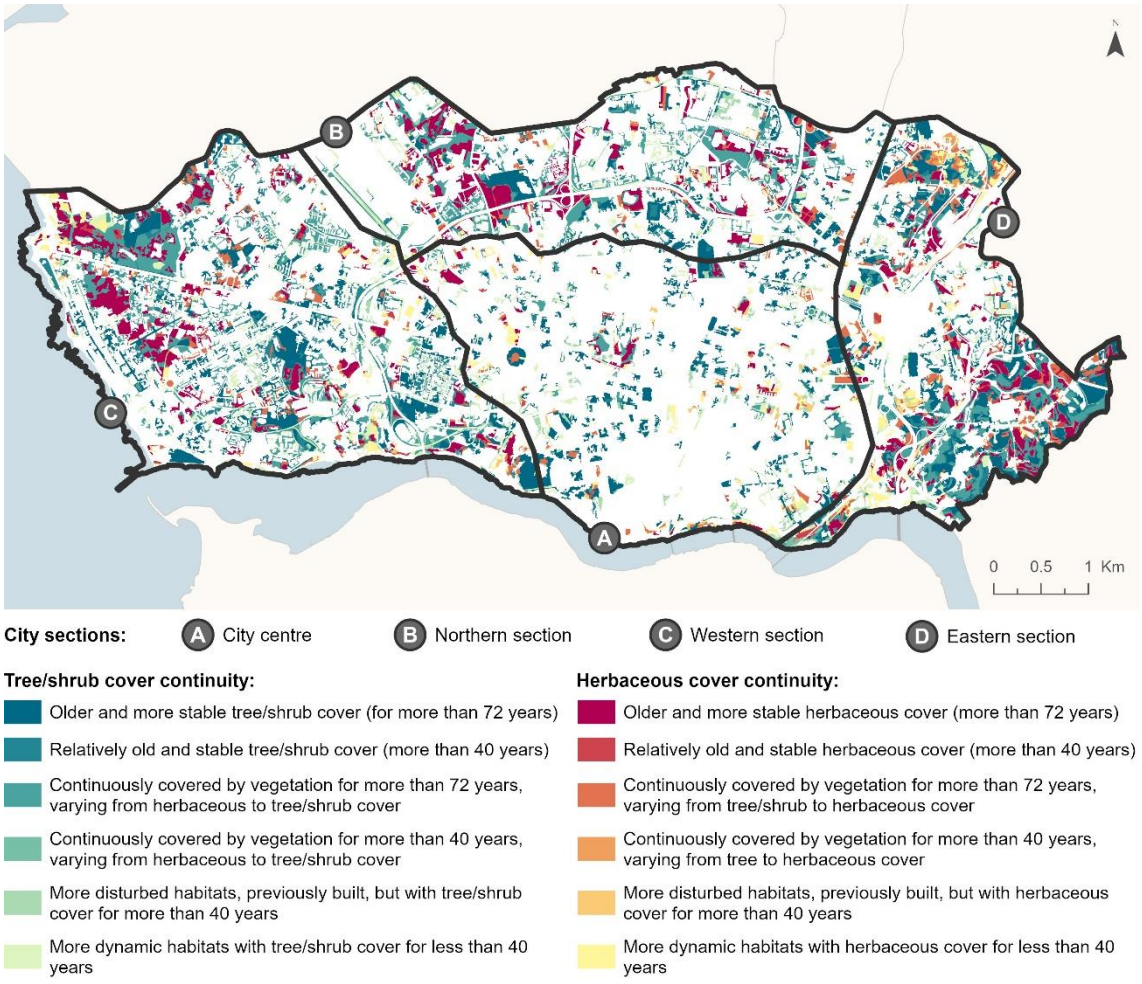



**Figure 5.1.** Temporal continuity of tree/shrub cover and herbaceous cover, in the different sections of the city.

The area here designated as the **city centre** (A in Figure 5.1, Box 5.1) corresponds roughly to the section of the city enclosed by the internal ring road (*Via de Cintura Interna*, VCI), with the exception of the portions of land with higher concentrations of green spaces that make the transition to the peripheral sections. The city centre is where urbanisation first happened, and it is nowadays the most densely urbanised area in Porto. Nevertheless, an interesting portion of vegetation patches, particularly tree/shrub cover, has persisted, mostly in small and isolated fragments, both in public gardens and in private green spaces within urban blocks. While public gardens were preserved throughout the decades, private green spaces near the centre have been gradually reduced, in number and size, and displaced by further urbanisation, increasing the already high levels of habitat isolation and fragmentation. A few larger patches of vegetation have also been preserved in public parks, some originating from former 19$^{th}$-century recreational farms. These larger parks are present only on the outside edge, at the intersection of the city centre with the other sections of the city, where they play a

pivotal role regarding green connectivity towards the city centre. Despite the high degree of urbanisation, some undeveloped land still persists in the city centre. The large dimension and central positioning, as well as the presence of older herbaceous patches, highlight the conservation value of these remnants; their preservation is fundamental, safeguarding as much vegetation as possible, in order to promote their benefits for citizens.

The **northern section** of Porto (B in Figure 5.1, Box 5.1) is delimited by the industrial area (to the west), Avenida Fernão de Magalhães (to the east), the city centre section (to the south), and Matosinhos municipality (to the north). This section presented a strong rural character in 1947, and substantial extensions of agricultural fields, with herbaceous crops, still existed in 1979. However, in just a few decades, there was a drastic increase in urban sprawl, and previously large and continuous herbaceous habitats were invaded and replaced by artificial built-up and impervious surfaces, causing a high degree of fragmentation and isolation of the remaining herbaceous patches. This section of the city possesses some of the most interesting herbaceous remnants of Porto; however, they are mainly located in undeveloped land, where they face an elevated risk of disappearing due to urban pressure. Unlike herbaceous habitats, tree/shrub patches have increased in this section, accompanying new urban developments and the abandonment of agricultural fields. Some older tree/shrub cover habitats are preserved in a few public parks and gardens, as well as in private green spaces associated with educational, health and other civic facilities.

The **western section** of Porto (C in Figure 5.1, Box 5.1), delimited by the Atlantic Ocean, Douro River, city centre and northern section, showed a varied scenario of different land covers and uses in 1947. The co-existence of agriculture, forestry and urbanisation created a balanced mosaic, where large patches of herbaceous and arboreal vegetation were occasionally crossed by impervious and built-up areas. Throughout the decades, urban growth originated an increase in fragmentation and isolation of vegetated habitats, but this section of the city is home to some of the larger green spaces of Porto today. While some tree/shrub cover, previously present in private gardens, was lost over time, a significant portion of the older tree/shrub cover was integrated into some of the most recognized parks and gardens of the city. Conversely, the extensive patches of older herbaceous cover that remain here, with some still managed as agricultural areas, occur mainly in undeveloped areas, being extremely vulnerable to further urbanisation.

The **eastern section** (D in Figure 5.1, Box 5.1) has a rich and diverse past, associated with agriculture (both herbaceous and wooded crops), forestry and industry, which are

economic activities that have been declining in Porto for decades. It is enclaved between the city centre, northern section and municipality of Gondomar, and its role in the movement of people and goods between the city centre and neighbouring areas has been accentuated in recent years, when several main roads cut through its territory. This was a favoured location for 19th-century recreational farms, and several still persist today, having been transformed into public or private green spaces. Agricultural practices are still present in this section of the city, especially near Tinto and Torto Rivers, but the abandonment of a large portion of herbaceous fields and pastures originated the proliferation of vacant lots, with no defined use. This is one of the green space types most prone to the loss of herbaceous habitats, where herbaceous vegetation can be replaced both by artificial elements after urbanisation processes or by wooded vegetation if ecological succession is not halted. On the other hand, vacant lots, especially in this eastern section, also represent an opportunity for delimiting and managing multifunctional green spaces benefitting human communities at various scales. In this section, biodiversity connectivity with the surrounding municipalities seems facilitated by the green and blue corridors created by the rivers and their riparian gallery, which promotes the dispersal and colonization of less mobile native species but can also facilitate the spread of invasive species from more urbanised areas.

### *5.1.2. Urban wildlife in Porto: current situation*

Considering the drastic changes in land cover, as well as the current scenario of urban habitat conservation in Porto, the city exhibits an expressive diversity of vertebrates. The vertebrate groups considered in this research (amphibians, reptiles, and birds) have very distinct life traits and ecological requirements. This leads to different responses to environmental change, however, in general, all studied groups seem to respond negatively to higher degrees of urbanisation, represented by the cover of artificial elements in chapter 4.

Amphibians and reptiles represent the most threatened groups of vertebrates, being particularly susceptible to land modification, such as urbanisation (Cordier et al., 2021; Delaney et al., 2021). Five amphibian species were detected during this research, with two species from the order Anura (common midwife toad *Alytes obstetricans*, Perez's frog *Pelophylax perezi*) and three species from the order Caudata (Bosca's newt *Lissotriton boscai*, marbled newt *Triturus marmoratus*, fire salamander *Salamandra salamandra*). According to previous studies (Barbosa, 2016; Guilherme et al., 2015), the

city of Porto is home to four additional amphibian species, but these did not appear in the sites sampled during this research (spiny toad *Bufo spinosus*, Iberian painted frog *Discoglossus galganoi*, western spadefoot toad *Pelobates cultripes*, palmate newt *Lissotriton helveticus*). The vulnerability of this group seems to be confirmed by the observed data and spatial predictions, presented in chapter 4, as amphibians do not occur in most of the study area, especially in the areas with more fragmentation and isolation of urban vegetated habitats, such as the city centre (section A, Figure 5.1). Most of the amphibian diversity in Porto is concentrated in the western section of the city, with some dispersed occurrences in the northern and eastern sections.

The presence and diversity of amphibians in Porto seem to be positively associated with older patches of arboreal vegetation with adequately maintained water elements, which occur mainly in urban parks and gardens. The low dispersal capabilities of amphibians hinder their colonization of recently created habitats, as was also highlighted in chapter 4, especially due to the lack of green corridors between the urban green spaces where amphibian populations still survive. On the other hand, their reduced home ranges and metabolic requirements facilitate that, provided that upland and aquatic habitats are favourable, populations will persist in the long term even in very small patches (Raquel Ribeiro, 2011). Based on the data collected, in this research and previous literature, the most important areas for amphibian conservation in Porto, and that could act as possible sources for recolonization of other areas, are Virtudes Garden, Botanical Garden, City Park, Serralves Park, Prelada Park, S. Roque Park, and Oriental Park, as they harbour two or more species of amphibians (Barbosa, 2016; Machado, 2014; Pereira, 2011; Raquel Ribeiro, 2011). Other green spaces also stand out for harbouring amphibians, although with a lower diversity (only one species), such as Nova Sintra Park, Covelo Park, Casa Tait Garden and Pasteleira Park (author's unpublished data; Ribeiro, 2011).

The reptiles in Porto seem to occupy a broader range of habitats than amphibians but are less diverse at the city level. Only four species were recorded during fieldwork, three from the family Lacertidae (Bocage's wall lizard *Podarcis bocagei*, Lusitanian wall lizard *Podarcis lusitanicus*, large psammodromus *Psammodromus algirus*) and one from the family Colubridae (southern smooth snake *Coronella girondica*). Reptiles are one of the least studied groups of vertebrates, particularly in urban areas (Faeth et al., 2011; Rega-Brodsky et al., 2022), and the same seems to be true for Porto. To the best of my knowledge, before this research, only three other studies focused on describing reptile communities in this study area (FCT project "Urban Green Structure: Study of the relation between public space morphology and flora and fauna diversity in the city of Porto"

[PTDC/AUR-URB/104044/2008], unpublished data; Pereira, 2011; Ribeiro, 2011), which detected three additional species (slow worm *Anguis fragilis*, horseshoe whip snake *Hemorrhois hippocrepis*, ocellated lizard *Timon lepidus*). More recently, some isolated records of other non-native reptile species (common wall gecko *Tarentola mauritanica*, Madeiran wall lizard *Teira dugesii*) have also emerged in Porto (Ferreira et al., 2023; R. Ribeiro, M. Carretero, personal communication), originating from introductions caused directly by human action. Among all reptile occurrences in Porto, it is worth mentioning the detection of *Psammodromus algirus*, since this species had not yet been recorded for this study area (Loureiro et al., 2010). This could be a sign of a shift or expansion in the distribution range of this species, probably due to climate change, in which species associated with Mediterranean environments (such as *P. algirus*) are expected to conquer new areas of favourable habitat, at the expense of species associated with Atlantic environments (S. B. Carvalho et al., 2010; Sillero, 2021).

Reptile occurrence and diversity seem to respond positively to areas with higher vegetation cover, both currently and in the past, even if that past vegetation was already greatly reduced, as described in chapter 4. This can help explain the spatial pattern of reptile diversity in the city of Porto: they seem to be more prevalent and diverse in the peripheral area of the city, particularly in the western and eastern sections (C and D, Figure 5.1), where vegetation is, or was, more abundant. Conversely, the city centre (A, Figure 5.1), which has been densely urbanised for decades, is almost devoid of reptiles, with only a few rare exceptions. Based on this research and previous literature, it can be stated that the most important areas for the conservation of reptiles in Porto are Quinta de Bonjóia, Nova Sintra Park, City Park, Serralves Park, Pasteleira Park, Botanical Garden, Casa Tait Garden, Prelada Park and Oriental Park, with multiple species of reptiles occurring in these areas. Other areas in the city seem to harbour only one of two species of lacertid reptiles: 1) *Podarcis lusitanicus* occurs only in a few areas near Douro River and habitats in its rocky margins, among which Palácio de Cristal Gardens and Virtudes Garden can be highlighted; 2) *Podarcis bocagei* is distributed in the peripheral sections of the city, occurring in parks and gardens, such as S. Roque Park, Covelo Park, Ramalde Sports Park, and Asprela Park, in agricultural areas, and even in small vegetation patches around residential developments.

Both amphibians and reptiles seem to exhibit a time-lagged response to the loss of vegetation, as they seem to persist in small-sized habitats, probably due to their reduced ability to disperse through the urban matrix to more favourable habitats. This could point to a situation of extinction debt for some herpetological populations. Amphibians appear

to have managed to maintain, in the last decade, a relatively stable, albeit low, abundance in the few habitats in which they survive, but their situation can quickly take a turn if their environment is further degraded or incorrectly managed. However, for reptiles, the extirpation of small populations has become more obvious in the same period, as previously known populations where no longer detected in this field campaign, and some of the populations in the more densely urbanised areas were extremely reduced. Although habitat loss and degradation are believed to play a major role in species disappearance, other factors, such as predation by pets and direct persecution, cannot be completely ruled out at this point.

Being the most diverse group of vertebrates, bird communities are relatively rich in urban areas and the same was observed for Porto, where 40 species were detected during this research (chapter 4). Complementing with other recent studies (FCT project "Urban Green Structure: Study of the relation between public space morphology and flora and fauna diversity in the city of Porto" [PTDC/AUR-URB/104044/2008], unpublished data; Pereira, 2011), this means that the accumulated total of birds recorded recently in Porto adds up to 75 species.

As expected, a significant proportion (17.5%) of the sampled bird species can be considered classic synanthropic species, i.e., they live in close association with humans and benefit from anthropogenic resources (Møller, 2009; Møller & Díaz, 2018; Tryjanowski et al., 2021). Some of these, like the common pigeon *Columba livia* and the yellow-legged gull *Larus michahellis*, benefit from the opportunity of both artificial nesting sites and food sources. They can reach extremely high abundances in the most densely urbanised areas of Porto, particularly in the city centre, where competition with other species is minimal, and have become a nuisance for human populations (Lyytimäki et al., 2008; Shochat et al., 2010). Others, such as the house martin *Delichon urbicum*, the barn swallow *Hirundo rustica*, and the black redstart *Phoenicurus ochruros*, are known for their traditional use of built elements for nesting but are not so abundant in the city of Porto, possibly due to the low availability of feeding habitats or even changes in architectural elements (Bowler et al., 2019; Murgui, 2002; Šálek & Mayer, 2023). During this research, some species were detected that are considered non-native to this study area (15% of the sampled species). Most of these result from deliberate or accidental introductions from captive individuals and some, such as the rose-ringed parakeet *Psittacula krameri*, the monk parakeet *Myiopsitta monachus*, and the Egyptian goose *Alopochen aegyptiaca*, were already known to have breeding populations in Porto. It is worth mentioning the record of one Iberian magpie *Cyanopica cooki*, a species whose

distribution in the literature corresponds to central and southwestern Iberian Peninsula, in association with Mediterranean habitats – can this also be a sign of an expansion or a shift in the distribution range due to the effects of climate change, as predicted by Araújo et al. (2012)?

The most diverse groups of birds in Porto seem to be open woodland and edge species (35% of the sampled species), and forest species (22.5%), which can be explained by the prevalence of tree cover in the territory. Forest species, such as the short-toed treecreeper *Certhia brachydactyla*, the coal tit *Periparus ater*, the Eurasian wren *Troglodytes troglodytes*, or the common firecrest *Regulus ignicapilla*, seem to particularly benefit from the presence of denser and more mature tree cover, which tend to be richer in invertebrates (as they are generally invertivore) and where they find tree cavities to nest (Janssen et al., 2017; Nordén et al., 2014). On the other hand, open woodland and edge species, like the European robin *Erithacus rubecula*, the European goldfinch *Carduelis carduelis*, the wood pigeon *Columba palumbus*, or the Eurasian jay *Garrulus glandarius*, tend to exhibit more generalist habits, as, while depending on tree/shrub cover for nesting, they generally resort to more diverse feeding sources (invertivores, granivores, omnivores) and sites (in lower vegetation, in the ground, in open spaces, etc.). The scarcity of some vegetated habitats in Porto is reflected in the bird diversity: there was only one native grassland species recorded (zitting cisticola *Cisticola juncidis*; 2.5% of samples species) and only one shrubland species (dunnock *Prunella modularis*; 2.5%), in very restricted locations. Although an interesting number of aquatic/marine species occur in Porto (Farinha-Marques et al., 2023; Guilherme et al., 2015), only two were recorded in this field campaign (common moorhen *Gallinula chloropus* and mallard *Anas platyrhynchos*; 5% of sampled species), as most sampled sites were distant from the ocean and large water bodies.

Generally speaking, bird species diversity seems to respond primarily to the presence of vegetation cover. Similarly to the other vertebrate groups, birds exhibit a positive association with current and older vegetation cover. However, unlike amphibians and reptiles, birds seem to also take advantage of recent vegetation patches, highlighting their increased dispersal abilities and adaptability to new habitats. This makes them the ideal target group for interventions dealing with habitat restoration and recovery of green spaces when fragmentation and isolation issues are not easily resolved.

### *5.1.3. Recommendations for the local planning and design of the urban green infrastructure*

After interpreting the spatial predictions regarding vertebrate species richness, as presented in chapter 4, and complementing with additional data obtained from already mentioned literature, it was possible to define in detail the most important areas for vertebrate conservation in Porto (Figure 5.2, Box 5.2) and classify them according to their priority score (Table 4.5, chapter 4). In Figure 5.2, the previously stated biological impoverishment of the city centre (section A) becomes obvious, while the western (C) and eastern (D) sections are richer in vertebrate species and the green spaces in which they occur.

**Box 5.2.** Examples of some of the main areas for vertebrate conservation (with fulfilled biodiversity value), for each of the city sections.

**MAIN AREAS FOR VERTEBRATE CONSERVATION**
**(FULFILLED BIODIVERSITY VALUE)**

**A. CITY CENTRE**

**Parks and gardens with public access:**
- Palácio de Cristal Gardens & Casa Tait Garden
- Covelo Park
- S. Roque Park
- Nova Sintra Park (all shared with the peripheral sections)
- Virtudes Garden
- Paulo Vallada Garden

**B. NORTHERN SECTION**

**Parks and gardens with public access:**
- Covelo Park
- Asprela Park
- Quinta de Lamas Park
- Requesende Park
- Arca d'Água Garden
- Sarah Afonso Garden
- Palmira Milheiro Garden

**Private green spaces and residential areas:**
- Prelada Park
- Conde de Ferreira Hospital
- Avides Moreira Park
- Asprela Campus
- Sta. Luzia residential area
- Prelada residential area

**Undeveloped land:**
- Prelada
- Viso / Requesende
- Telheira
- Regado
- Lamas
- Areosa Ocidental

**C. WESTERN SECTION**

**Parks and gardens with public access:**
- City Park
- Serralves Park
- Pasteleira Park
- Passeio Alegre Garden
- Botanical Garden
- Palácio de Cristal Gardens & Casa Tait Garden
- Ramalde Sports Park

**Private green spaces and residential areas:**
- Magalhães Lemos Hospital
- António Cardoso / Guerra Junqueiro
- Campo Alegre Campus
- Pasteleira residential areas
- Pinhais da Foz
- Foz Velha (Montebelo)
- Campinas
- S. João Brito

**Undeveloped land:**
- Ribeira / mata de Aldoar
- Ribeira de Nevogilde
- Ribeira da Ervilheira
- Aleixo
- Via Panorâmica

**D. EASTERN SECTION**

**Parks and gardens with public access:**
- S. Roque Park
- Alameda Cartes Park
- Quinta da Bonjóia
- Oriental Park
- Nova Sintra Park

**Private green spaces and residential areas:**
- Quinta da China
- Quinta da Revolta
- Quinta do Freixo
- Quinta das Areias
- Quinta de Salgueiros (Antas)
- Monte da Bela
- Cerco do Porto
- Contumil
- Rodrigues Semide Park

**Undeveloped land:**
- Areosa Oriental
- Ranha / Currais
- Contumil
- Tirares / Pego Negro
- Areias / Furamontes
- Granja
- Azevedo
- Monte da Bela
- Pinheiro de Campanhã
- Rêgo Lameiro / Formiga

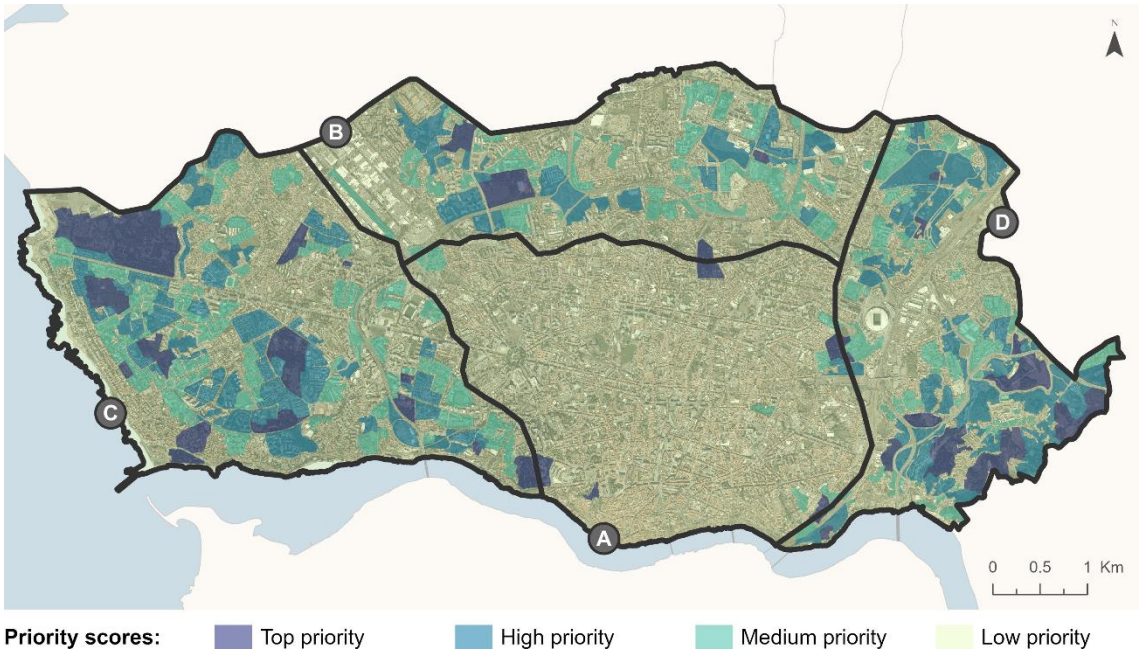



**Figure 5.2.** Priority areas for vertebrate conservation, considered at the neighbourhood and site scale, for each of the city sections (background imagery: Direção Geral do Território, 2018).

These areas can be considered the **biodiversity hotspots** of Porto; they are of utmost importance to maintain and improve the ecosystem services, sustainability and, ultimately, the quality of life of citizens in the city of Porto, and their **conservation** should be foreseen in legal urban planning instruments and environmental strategies of the municipality. Regarding their diversity of vertebrate species, conservation measures should be particularly aimed at the most vulnerable species, such as amphibians and reptiles, as these groups are largely dependent on these mostly peripheral green spaces for their city-wide conservation; the preservation of these areas will also have an "umbrella effect" on other species not analysed here. In this regard, it is recommended that a **diversity of small-scale habitats** is maintained, including herbaceous and arboreal habitats (preferably with a **higher temporal continuity**), as well as favourable breeding, refuge and feeding sites, adequate for the target species. For instance, regarding amphibian conservation, water elements should be more prevalent in urban green spaces, and these must have an adequate structure that allows the entry and exit of breeding adults and newly metamorphosed juveniles. Moreover, the management and maintenance plan of water elements must have amphibian populations into account and the introduction of ornamental fish should be avoided. The time-lagged response to habitat loss and degradation observed in certain species underscores the necessity of not only conserving existing green spaces in their current state, but also the relevance of **restoring and expanding habitats** in order to prevent probable local extinctions.

Additionally, to ensure viable vertebrate populations, the **physical connectivity** between priority sites should also be considered in long-term plans, which must be guaranteed by **continuous green corridors** as much as possible, since the most important target species (amphibians and reptiles) have reduced dispersal capabilities (R. Ribeiro et al., 2011). Birds also present a higher diversity in these spaces, but although they do not require a high degree of physical connectivity, it is recommended to **increase areas of grassland and shrubland habitats** to maintain and improve bird species diversity at the city level.

The observed data and the modelling results presented in chapter 4 confirm the validity of considering habitat temporal continuity as an indicator of species richness, used here as a proxy for urban habitat conservation value, as was proposed in chapter 3. All areas identified in Figure 3.7 as areas with higher habitat continuity are also identified as areas with higher species diversity in Figure 4.3, except for the green areas in the city centre (section A, Figure 5.2). Here, the results suggest that the negative effects of habitat loss, degradation, fragmentation, isolation, and disturbance from the surrounding urban matrix surpassed the beneficial effects of older vegetation patches for most vertebrate species.

Nonetheless, even in these cases of low species diversity, identifying the habitats with higher temporal continuity allows for the prioritization of areas for ecological improvement to increase the presence of vertebrate species in the urban territory. In the case of Porto, most of these areas correspond to small, simplified, and disturbed public parks and gardens, as well as small-scale private green spaces in complex patterns amidst the urban fabric (Figure 5.3, Box 5.3). Several authors have pointed out the relevance of small green spaces in city centres, especially if they are managed with differentiated practices aimed at biodiversity conservation and promotion (e.g., Shwartz et al., 2013).

Currently, according to fieldwork and modelling results, these areas present very low vertebrate diversity, and only the most tolerant species, such as *Columba livia* or *Larus michahellis*, are able to survive in the city centre, where they take advantage of anthropogenic resources and the lack of competition with other species. However, the presence of a few older vegetation patches, and therefore the extant biological legacy, increases the probability of success of interventions aimed at enhancing habitat structure, composition and management practices. Thus, it is recommended that **areas with biodiversity potential**, i.e. areas that have higher temporal continuity but lower species richness, are to be considered as a **priority for ecological restoration**.

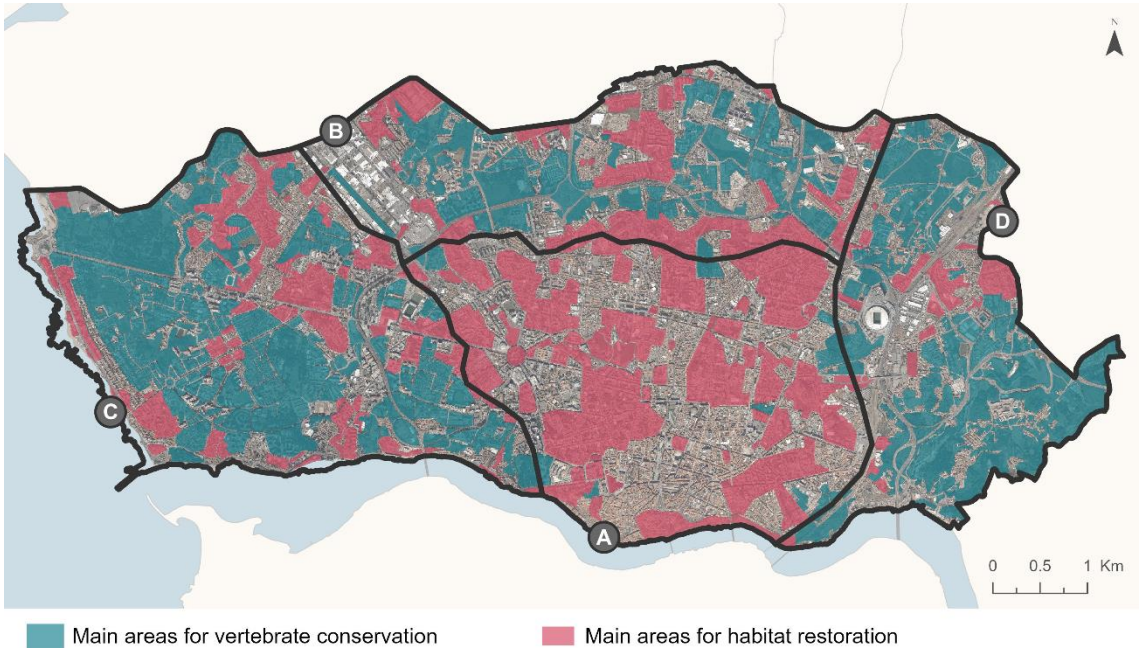



**Figure 5.3.** Main areas for vertebrate conservation (Box 5.2) and main areas for ecological restoration (Box 5.3), for each of the city sections (background imagery: Direção Geral do Território, 2018).

Additionally, they seem to be particularly important for strengthening the **connectivity** between larger and richer green spaces, especially in densely urbanised areas. As such, due to their value as potential habitats, dispersal corridors or steppingstones, it is recommended that these areas also integrate biodiversity conservation plans, as they should be preserved, improved and, ideally, expanded. Their relevance seems to be particularly higher in Porto's city centre, as the scarcity of urban green spaces greatly affects the occurrence of biodiversity. The larger and richer public green spaces (Palácio de Cristal Gardens, Covelo Park, S. Roque Park and Nova Sintra Park), in a borderline position in this section of the city, could act as a source of dispersal and contribute to the establishment of vertebrate populations in the city centre. These measures would be particularly relevant for birds, which can more easily adapt to newly intervened habitats and overcome dispersal barriers more easily. Again, conservation measures should be defined according to target species; for example, besides improving habitat structure, cavity-nesting forest birds would benefit from the setup of nest boxes. Moreover, in the context of a multifunctional urban green infrastructure, the establishment of more public gardens in the city centre, within walking distance for most residents, would not only benefit biodiversity conservation but would also provide additional benefits for the quality of the urban environment and human health and wellbeing (Ossola, Jenerette, et al.,

2021), in accordance with the later international recommendations regarding access to green spaces (World Health Organization, 2017, 2021).

**Box 5.3.** Examples of some of the main areas for ecological restoration (with unfulfilled biodiversity potential), for each of the city sections.

**MAIN AREAS FOR ECOLOGICAL RESTORATION**
**(UNFULFILLED BIODIVERSITY POTENTIAL)**

**A. CITY CENTRE**

**Parks and gardens with public access:**
- Carregal Garden
- Cordoaria Garden
- Praça da República Garden
- S. Lázaro Garden
- Marquês de Pombal Garden
- Rainha D. Amélia Garden
- Praça Francisco Sá Carneiro Garden
- Rotunda da Boavista Garden

**Private green spaces and residential areas:**
- Santa Catarina / Fontinha
- Cedofeita / Miguel Bombarda
- Avenida França / Oliveira Monteiro
- Av. Rodrigues Freitas / Heroísmo
- Antas / Combatentes
- Antero Quental / Faria Guimarães

**Undeveloped land:**
- Francos
- Lapa / Burgães
- Lima
- Fontaínhas
- Godim / Bonfim

**B. NORTHERN SECTION**

**Private green spaces and residential areas:**
- Quartel Viso
- Prelada Park
- Conde de Ferreira Hospital
- Asprela Campus
- Viso residential area
- Regado / Amial
- S. Tomé / Carriçal
- Carvalhido
- Campo Lindo

**Undeveloped land:**
- Telheira / Amial
- Azenha
- Areosa Ocidental
- Salgueiros / Aug. Lessa
- Barrocas

**C. WESTERN SECTION**

**Parks and gardens with public access:**
- Gardens of the Atlantic front (Avenida Brasil / Montevideu)

**Private green spaces and residential areas:**
- Nevogilde sea front
- Foz Velha (Cadouços / Cantareira)
- Condominhas
- Grijó / Boavista
- Pinheiro Manso / Mota Pinto
- Ramalde Baixo / Andresas
- Fonte da Moura
- R. Jornal Notícias / Lidador

**Undeveloped land:**
- Encosta da Arrábida

**D. EASTERN SECTION**

**Parks and gardens with public access:**
- Corujeira Garden

**Private green spaces and residential areas:**
- Eng. Machado Vaz
- S. Roque Lameira
- R. S. Roque / Circunvalação

**Undeveloped land:**
- Cartes / Maceda
- Vila Cova
- R. S. Roque / Circunvalação

Given the high degree of densification of built elements and impervious surfaces in the city of Porto, and its ongoing increasing trend, the areas that have not yet been through urbanisation processes and retain a larger proportion of permeable soil and vegetation have become even more valuable. In the context of this thesis, it is recommended that larger and less fragmented green areas, particularly those with a higher habitat continuity, be considered a priority for safeguarding the natural heritage of the city of Porto, as recreating complete ecological communities or habitats after their loss is

seldom feasible, and it's more efficient to preserve existing biodiverse areas rather than trying to recreate them in the future (Parris et al., 2018)

While the importance of public parks and gardens is already acknowledged in spatial planning policies in Porto, the same cannot be said about undeveloped land. Urban progress and biodiversity conservation can be compatible, but it is fundamental to safeguard older habitats and limit future urban developments. For that reason, it is essential to impose, at a municipal level, measures that would, at least, prevent further biodiversity loss, similar to what is already applied in other cities. For example, London is implementing the concept of "biodiversity net gain" regarding new developments, which was introduced by the Environmental Act of 2021 and requires that any new urban development project generates an expected increase of 10% in biodiversity indicators, preferably on-site (Greater London Authority, 2021; Stephens, 2024). In a European Union context, the "Biodiversity Strategy for 2030" encouraged cities to incorporate biodiversity and green spaces in their strategic and legal instruments and promoted the creation of the "Green City Accord" to guide cities to implement greening plans (European Commission, 2021). The Municipality of Porto is one of the signatories of the European "Green City Accord" and has shown growing commitment to tackling diverse environmental challenges. For instance, climate change adaptation and mitigation have been addressed in several initiatives (e.g., Município do Porto, 2016), which is commendable. However, in a similar situation to other cities (Butt et al., 2018), the topics of biodiversity conservation and habitat restoration seem secondary as they are not explicitly promoted while being central to ecosystem functioning, climate resilience and human wellbeing (Campbell et al., 2009; R. M. De Carvalho & Szlafsztein, 2019; Knight et al., 2021; Oliver et al., 2015). At the moment, Porto Municipality is developing the "Environmental Index of Porto", which has been anticipated in the Municipal Master Plan (Câmara Municipal do Porto, 2021c), based mainly on circular economy, energy efficiency and climatic comfort of new buildings (Câmara Municipal do Porto, 2020a). However, as "ecological" building codes do not often deliver benefits for biodiversity (Parris et al., 2018), a new "Biodiversity Index" is here proposed to motivate urban developers and promoters to intentionally include biodiversity conservation matters in their plans and designs, aligned with the objectives of the "Green City Accord". The plans and designs for new urban developments should include the on-site preservation of a significant proportion of permeable soil, conservation and/or restoration of existing habitats, promotion of native flora and fauna species, and reinforcement of green connectivity with surrounding sites, which would also have benefits on human health and

wellbeing and the economic value of real estate. In this regard, Garrard et al. (2018) developed a framework for implementing biodiversity-sensitive urban design, guiding urban designers to reconcile biodiversity and urban development objectives. Other authors suggest that biodiversity should even be considered as a non-human stakeholder regarding urban developments (Hernandez-Santin et al., 2023). While potentially adequate in already densely urbanised areas, the adoption of isolated greening measures, such as green roofs and walls, has questionable benefits for the conservation of low mobility taxa (Lepczyk et al., 2017) and cannot compensate for the detrimental effects of the loss of a permeable green space on environmental conditions and human health, especially when considering older habitats and a richer biological legacy.

## 5.2. Limitations and future research

This thesis aimed to become the starting point for an in-depth reflection on the conservation of green spaces and biodiversity in the city of Porto and to fuel a discussion between urban ecologists, landscape architects, spatial planners, and city-dwellers. However, due to time, logistic and methodological constraints, some limitations have arisen during this research, which can have implications for the results and conclusions.

One of the goals of this research was to capture the dynamic nature of urbanisation in Porto during the last century. The available data and timeframe of this project allowed for a definition of intervals of around 30–40 years to study the evolution of the territory. While these were adequate to obtain a general overview of the land cover trajectories, shorter intervals would be appropriate to achieve a more accurate portrait of the areas with a higher land cover turnover.

The land cover mapping and classification were also accomplished with a simplified methodology and accounts only for broad land cover categories. This was a consequence of the use of older remote sensing imagery, which, due to its low resolution, black and white colouration, and vertical perspective, only allows for a minimal analysis of the top-most layer of land cover. Dominant plant species, different vertical vegetation strata, or the overlap between different land covers could not be assessed. This can cause, for example, the limited interpretation that all tree cover coincides with permeable soil when it can also occur in paved areas. Still, if needed and if complementary data is available, a more detailed description of patches, including habitat structure and

composition, can be pursued, as it is already foreseen in UrHBA methodology (Farinha-Marques et al., 2015, 2017).

The species richness of selected vertebrate groups was used in this research as a measure of biodiversity, as it simplifies data collection and is easy to communicate to non-experts, providing a rapid assessment of conservation value in a prioritization scheme. However, several authors have recognized the limitations of species richness estimates in addressing communities with different species compositions, which can have practical implications in a correct evaluation of conservation value. As such, for the development of biodiversity conservation plans, species richness should be complemented with information about species' abundance, redundancy, functional roles, origin (native or non-native), invasiveness, rarity, endemism, or sensitivity to environmental changes (Fleishman et al., 2006). Ideally, the distribution of each individual species would be analysed, which would allow a more detailed description of species assemblages, as well as a clearer definition of relationships between the presence of each species and the land cover legacy; however, this modelling procedure was made impossible by the reduced number of records. Likewise, despite the apparent precision of the spatial predictions, the statistical robustness of the modelling results was also affected by limited species' occurrences. Nevertheless, the results of this thesis can be useful to explore the spatio-temporal connectivity of the green space network of Porto (Martensen et al., 2017; Uroy et al., 2021) and to anticipate future scenarios for the diversity of vertebrates in Porto based on land cover change (Bastos et al., 2012; Newbold, 2018).

## 5.3. Concluding remarks

In this thesis, the relevance of a temporal approach to urban landscapes has been demonstrated, regarding biodiversity conservation. In one way or another, all selected vertebrate groups have revealed a relationship with past land cover or land cover age. While birds seem more adaptable to land cover change, amphibians and reptiles show a delayed response to habitat loss and fragmentation, which makes them more vulnerable to local extirpation events even without further habitat change.

In addition to contributing to the understanding of the urban ecosystem, in particular the relationship between biodiversity levels and land cover change, this thesis also aimed to contribute to narrowing the gap between ecological sciences and urban planning, by

generating “actionable knowledge”, i.e. information useful to planners, managers, and decision-makers. This was accomplished due to several aspects that shaped this research, namely: 1) the fine scale of analysis is close to the scale of direct intervention in urban space; 2) the use of land cover as an indicator of broad habitat types is pertinent since land cover can be directly transformed in most urban interventions; 3) the representation of ecological data in spatially-explicit and visual formats facilitates the transfer of knowledge between the disciplines and allows for the development of spatial prioritization strategies. Moreover, besides sharing ecological data on urban biodiversity, this thesis also intended to provide urban planners and managers with a method to identify priority areas for biodiversity conservation and regeneration (as demonstrated in chapter 3 and validated in chapter 4), even when the means or resources for species sampling are not easily available, namely urban biodiversity experts.

The results here presented are particularly informative for the future planning and management of the urban territory of Porto. They can also provide a baseline for the development of a monitoring program on urban biodiversity conservation and for the outline of a municipal biodiversity strategy. Nevertheless, the methods, findings and recommendations produced by this research can be useful for a variety of cities with a similar context, aiming to preserve urban green areas, limit inefficient land consumption and promote a more sustainable urban environment.

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# Appendices

## Published articles

**Article I**

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*Article*

# Looking Closer at the Patterns of Land Cover in the City of Porto, Portugal, between 1947 and 2019—A Contribution for the Integration of Ecological Data in Spatial Planning

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**Abstract:** As more people reside in cities and metropolitan areas, urban vegetation assumes an increasingly important role as one the main providers of ecosystem services in close proximity to human agglomerations. To improve the conditions for citizens and to optimise the sustainability of urban areas, the fields of landscape and urban ecology need to address the urgent priority to integrate ecological data in spatial planning, design, and management programs. With the objective to produce "actionable knowledge" for urban planning in the city of Porto (Portugal), we analyse the evolution of land cover since the mid-20th century at a fine spatial scale. Porto has followed the global trends of urbanisation, marked by a general increase in built-up and impervious surfaces that conquered the previously rural surrounding areas. This caused a severe decline in vegetation cover (especially herbaceous), as well as an increase in fragmentation and isolation of the remaining vegetation patches. These outcomes provide a detailed analysis of the city spatial dynamics, generating valuable information that can be relevant for future interventions regarding urban landscape change at a local scale, the most relevant for planning.

**Keywords:** landscape change; urban dynamics; spatial metrics; urban habitats; UrHBA

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## 1. Introduction

The concept of landscape is complex and manifold, having been appropriated by numerous disciplines, from the arts and humanities to the natural sciences [1–3]. For the purpose of this study, landscape is "an area, as perceived by people, whose character is the result of the action and interaction of natural and/or human factors" [4]. The landscape is inherently complex, heterogenous, and dynamic [1,5,6] and it requires a strong simplification into smaller spatial units to be comprehensively analysed [3,7]. The landscape is characterised not only by the physical attributes of the land but also the human experience of it, i.e., by its composition, pattern, and relationship between its components, as well as the perception of all these factors [6,8].

Urbanisation is one of the main generators of change in landscape patterns and composition, as it generally implies the spread and/or densification of built-up and impervious surfaces and the loss and fragmentation of vegetation, natural habitats, and agricultural land [9,10]. This, in turn, negatively affects the biodiversity levels [11–13], environmental conditions [14–19] and quality of life in urban areas [20–22]. Particularly in urban

environments, vegetation can be considered one of the most important contributors to environmental conditions, impacting the regulation of temperature, mitigation of flooding episodes, carbon sequestration and storage, adsorption of pollutants, provision of habitats for biodiversity, and supply of green spaces for recreation [14,20,23,24].

Cities and metropolitan areas are becoming more and more important in the context of the evolution of the human global population. In the mid-20th century, urban areas were populated by only around 30% of the global population (0.75 billion people); nowadays, around 55% of all humans live in urban settlements (4.22 billion people), as reported by the United Nations [25]. In 2050, it is estimated that around 68% of the world's people will be urban dwellers (6.68 billion)—in fact, it is expected that all of the future growth in world population will be located in urban areas [25].

In the face of the rise in urban population, the Sustainable Development Goals of the United Nations highlight the need to pursue sustainability in urban centres, through the creation or transformation of cities so that they are greener, less polluted, and more resilient to climate change, ecological invasions, and emergent diseases, in order to increase the health and quality of life of their citizens and minimise the effects of natural disasters [26–28]. To achieve sustainable cities, the discipline of Landscape Ecology can play a central role in the multidirectional transfer of knowledge between ecological research and urban planning [29]. However, when compared to their natural counterparts, urban ecosystems generally present a very complex, heterogeneous, and dynamic landscape, driven by a multitude of interacting social, economic, and environmental factors, which translates into additional challenges for spatial planning and management [30]. Furthermore, there is often a mismatch of temporal and spatial scales, where the time and land units for planning and management decisions do not coincide with the ecological processes [29,30]. These factors can introduce barriers to the "knowledge to action" process, where both ecological research and policies at a broad scale (international or national level) are difficult to translate to the local level [29,31,32]. The "local level" can be defined as the physical areas that are directly intervened by urban planners, designers, managers, and users [29]. In urban contexts, the ecological dynamics of the landscape are largely affected by local scale decisions such as the planning and design of individual sites, infrastructures, and community masterplans [33]. At the local level, historical data about the environmental conditions of each site can also present important ecological opportunities and constraints; for example, historic ecological data often serve as an inspiration for urban design and landscape architecture projects, regarding ecosystem performance and aesthetic expression [33].

Most ecological research is focused on the advancement of academic knowledge, intended to inform policies at a broad scale, but with limited value for landscape planning at the city or neighbourhood level. Accordingly, most spatial planning and management programs fail to integrate ecological data [32–34]. Thus, it is imperative that scientists, planners, designers, communities, and other local stakeholders work collaboratively, creating and transferring knowledge in a format that is clear and useful for every thematic field, in an effort to advance the field of sustainable landscape planning [31,32,35–37].

In highly heterogeneous and dynamic regions, such as urban areas, ecological research must adapt a fine spatial scale and seek detailed temporal information that can be complemented with diverse social, economic, cultural, and political data, which are crucial to inform landscape planning and design, adjusted to the local context of each city [29,33]. In this sense, the study of land cover facilitates the quantitative analysis of the spatial patterns of vegetation and acts as a proxy for habitat distribution [20]. Land cover can be defined as the physical material that covers the surface of the landscape, usually related to vegetation types or artificial structures [38]. The concept of land cover is easily applicable everywhere as it transcends local conditions [39], but on the other hand, it is relevant at a local scale as it can be directly transformed through most urban interventions, not necessarily requiring a change in land use type. In contrast, land use classification, often used in urban ecological studies, is difficult to associate with biodiversity, habitat, and environmental conditions, as the relationship with vegetation cover remains unclear.

These challenges seem to be particularly relevant in compact cities [40–43]. As these undergo processes of densification, adequate policies regarding sustainable urban planning, advocating for habitat and biodiversity conservation while offering a suitable quality of life for residents, become imperative as there is (literally) no room for error. In this urban context, there is a pressing need for a concerted effort between multiple disciplines and professionals to generate useful knowledge, closer to the scale of intervention, in order to come up with innovative and tailor-made actions fitted to the local context.

With this in mind and using a compact city from the temperate region as a case study (Porto, Portugal), we analysed the change in urban land cover for an approximate period of 70 years. Our general intention was to produce "actionable knowledge" [35] with a fine spatial scale and vast temporal span. Thus, our research objectives were to (1) assess the land cover of Porto for three representative dates encompassing the main landscape changes, from the mid-20th century to recent days; (2) analyse the evolution of landscape pattern and composition with spatial metrics; and (3) identify the main trends, at a small scale, that could inform local plans and support direct actions taken by local governance and management systems for a more sustainable city.

## 2. Materials and Methods

### *2.1. Study Area*

This study focuses on the Municipality of Porto, Portugal, in Southwestern Europe (Figure 1). The city is located in Northern Portugal, at the intersection of the Douro River with the Atlantic Ocean, where the temperate climate, with mild temperatures year-round and higher precipitation in the winter (Csb regime, according to the Koppen–Geiger classification system [44]), benefits a diverse community of plant species and habitats for European standards. The latest climate records indicate a mean annual temperature of 15.3 °C and total annual precipitation of 1174.0 mm (data for 2021 [45]).

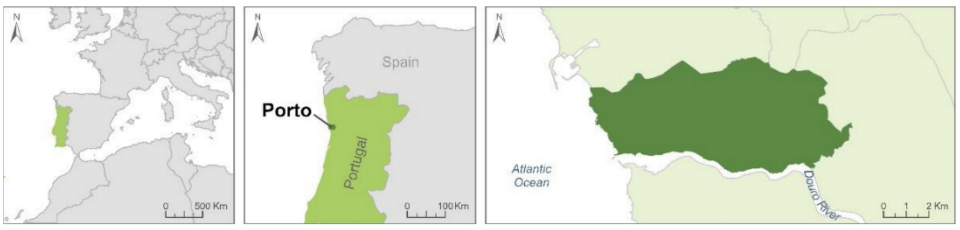



**Figure 1.** Location of the city of Porto, Portugal.

The region has been occupied since pre-historic times, but it remained a small and compact urban centre, surrounded by agriculture and forest, until the 19th century. In contrast, the industrial development in the 20th century boosted the expansion of the built-up area to its administrative limits, forming an urban continuum with the adjoining municipalities [46]. Despite its limited size (around 42 km$^2$ and almost 232,000 inhabitants [47]), Porto is currently the dynamic core of a metropolitan area composed of 17 municipalities, housing 1.7 million residents [48].

### *2.2. Land Cover Mapping and Classification*

One of the main purposes of this study was to quantify the change in land cover of Porto considering a substantial time interval, based on historic remote sensing data. With this in mind, we decided to use three moments in time: one for the present time, one for a distant past (going as far back as possible with reliable data), and one intermediate moment. As far as our knowledge goes, the oldest aerial photography covering the city of Porto dates back to 1939, and it is available for consultation in the archives of the municipality. However, that first survey had substantial gaps, not covering the entire territory, and was executed during the winter, which makes it difficult to record deciduous vegetation;

for these reasons, the aerial photograph of 1939 was not used for this study. The next oldest record corresponds to the 1947 photography obtained from Centro de Informação Geoespacial do Exército. The recent records of land cover in Porto were analysed based on the 2019 satellite photography, accessed through Google Earth. For the intermediate moment, considering similar intervals from the first and to the last moment, the 1979 aerial photography was selected, and it was made available for this study through a collaboration with the Municipality of Porto. Thus, the land cover for the city of Porto was analysed, through the interpretation of aerial and satellite imagery, in vectorial format in GIS software (ArcMap Desktop 10.5) for three different years: 1947, 1979, and 2019.

In order to have aerial photos as georeferenced raster layers in a GIS, original images must be orthorectified [49,50]. In the case of historical photos, this task may pose several difficulties due to the lack of knowledge about technical aspects of the aerial cameras used and also due to the difficulty in finding common points to present time images for a proper image georeferencing. Pinto et al. [50] propose a methodology based on individual photos, requiring a minimum number of 6 ground control points (GCPs) per photo. In the case of the 1947 photos, in a total of 24, finding the required number of GCPs would be difficult due to the changes that occurred in the city. Another methodology, proposed by Gonçalves [49], applicable to a standard coverage of aerial photographs with 60% overlap, requires a minimum of 4 points to georeference a block of images. It makes use of the structure from motion (SfM) strategy, now largely used for orthorectifying images acquired by drones. The method was applied with the Agisoft Metashape program [49]. It starts with the application of computer vision algorithms to find common points between overlapping images, generates a point cloud and a 3D model of the terrain, which is georeferenced in a block by a set of GCPs that perform 3D translation, rotation, and scale. Figure 2a,b represents a typical GCP in a garden that kept its original shape in the 1947 photo and in present time orthoimages. A set of 6 GCPs were used, resulting in residuals which can be used as a quality control of the georeferencing process. A root mean square error smaller than 2 m was obtained, which was considered appropriate for the analysis to be carried out. This is followed by a set of additional processing steps, resulting in a final orthomosaic, which can be inserted in the GIS and overlaid with other georeferenced data. Figure 2c shows a sample of the orthomosaic with vector polygons of building blocks. The quality of the orthomosaic geolocation was considered appropriate for a precise combination with other GIS data layers.

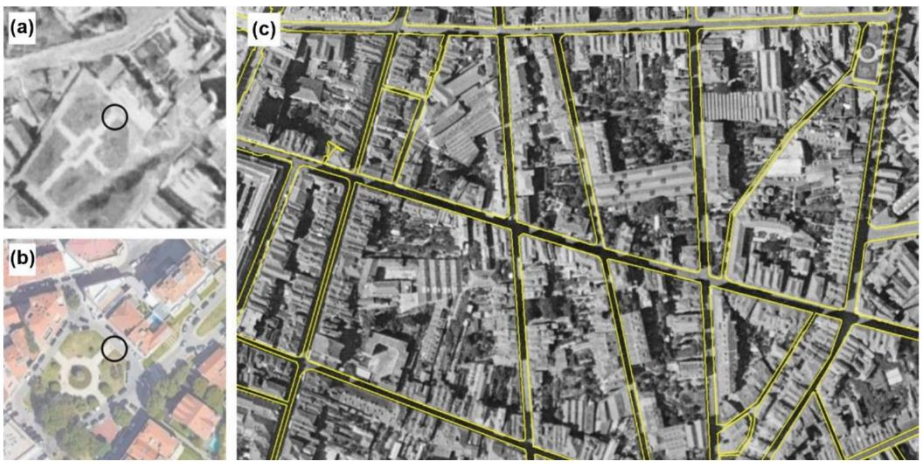



**Figure 2.** (**a**) Examples of a GCP in the 1947 aerial photo; (**b**) the same point in present time orthoimages; (**c**) large portion of the final orthomosaic, with overlaid vector data of building blocks in a GIS, showing the accurate geolocation of the orthomosaic.

Land cover was classified with a version of the UrHBA method [39], streamlined for exclusive use with remote sensing data, especially considering the low resolution and black/white colour of the older photographs. UrHBA is a spatially explicit method, based on the visual interpretation of the landscape, designed to describe urban environments in a fine scale, making it particularly oriented for scientific research, urban planning, and data communication. Unlike traditional classifications of urban land that rely on land use data, UrHBA is based exclusively on land cover, which has a direct relationship with the presence or absence of vegetation. The classification of land units based on life traits of vegetation (instead of species or botanical communities) makes the method easily applicable in a wide range of geographical contexts. If necessary, the method allows for a more thorough characterisation later on, with the addition of detailed attributes, which should be obtained through fieldwork. The land cover categories used in this study are (1) Artificial Built Elements, ABE; (2) Trees and Shrubs, TRS; (3) Herbaceous, HER; (4) Sparsely Vegetated—Terrestrial, SPV; and (5) Sparsely Vegetated—Aquatic, AQU (Table 1). These were adapted from Urban Habitat Categories and super-categories from UrBHA (for further detail and definition of the categories, see [39,51]). The mapping procedure was also simplified—all elements were mapped as patches, even if with a linear shape; the minimum dimension for patches to be distinguished was 2000 $m^2$, and the minimum width was 5 m.

**Table 1.** Land cover categories (adapted from [39]).

| Land Cover Categories | Abbreviation | Description |
|---|---|---|
| Artificial Built Elements | ABE | Impervious surfaces, buildings, and other constructed elements. |
| Trees and Shrubs | TRS | Woody vegetation, including all phanerophytes and shrubby chamaephytes. |
| Herbaceous | HER | Herbaceous vegetation, including hemicryptophytes, therophytes and geophytes. |
| Sparsely Vegetated—Terrestrial | SPV | Every type of non-vegetated soil, such as bare soil, sand, and rock. |
| Sparsely Vegetated—Aquatic | AQU | Every type of water surface, such as the sea, rivers, lakes, and ponds (including artificial elements). |

### *2.3. Spatial Metrics*

Land cover patterns were monitored by means of spatial metrics, which can be used as indicators of habitat availability, shape, fragmentation, and connectivity. For the purpose of the generation of spatial metrics, the term "patch" corresponds to the smaller spatial unit with homogeneous land cover, "class" consists of the group of all patches with the same land cover, and "landscape" identifies the entire study area, formed by a heterogeneous mosaic of patches [52].

Spatial metrics were calculated with V-LATE 2.0 beta [53] for the three resulting maps of land cover classification, at landscape, class, and patch levels. For landscape-level analysis, all patches are considered for the calculations, i.e., all the different land cover categories are included in the same analysis; at the class-level analysis, individual calculations are performed for each land cover category; and at patch-level, a series of metrics is generated for each land cover patch. This software uses vectorial data for the calculation of the most common metrics, and a few were selected as indicators of composition and configuration of the urban landscape, as shown in Table 2. These metrics can be grouped as (1) area and edge metrics—fundamentally related to the basic dimensions of patches, such as area and perimeter, and important for the analysis of habitat availability, fragmentation, and edge effects; (2) shape metrics—related to patch morphology and

geometric complexity, which can influence edge effects, animal migration, and plant colonisation processes; (3) aggregation metrics—these indicate the tendency of patch types to be more or less dispersed and separated in the landscape, also known as "landscape texture", influencing a diverse array of ecological processes, especially those concerning habitat loss, fragmentation, and isolation; (4) diversity metrics—important to understand the landscape composition, and only calculated for the landscape level of analysis [52].

**Table 2.** Landscape metrics selected for this study (adapted from [52,53]).

| Level | Type | Metric |
|---|---|---|
| Landscape | Area and edge metrics | TA: Total area (ha)<br>LPI: Largest patch index (%)<br>MPS: Mean patch size (ha)<br>MPE: Mean patch edge (m)<br>ED: Edge density (m/ha) |
| | Shape metrics | MPAR: Mean perimeter–area ratio<br>MSI: Mean shape index<br>MFD: Mean fractal dimension |
| | Aggregation metrics | NP: Number of patches<br>MENND: Mean Euclidean nearest neighbour distance (m)<br>MPROX: Mean proximity index |
| | Diversity metrics | CR: Class richness<br>SHDI: Shannon's diversity index<br>SHEI: Shannon's evenness index |
| Class | Area and edge metrics | CA: Total class area (ha)<br>CP: Class proportion (%)<br>LPI: Largest patch index (%)<br>MPS: Mean patch size (ha)<br>MPE: Mean patch edge (m)<br>ED: Edge density (m/ha) |
| | Shape metrics | MPAR: Mean perimeter–area ratio<br>MSI: Mean shape index<br>MFD: Mean fractal dimension |
| | Aggregation metrics | NP: Number of patches<br>MENND: Mean Euclidean nearest neighbour distance (m)<br>MPROX: Mean proximity index<br>DIV: Division index |
| Patch | Area and edge metrics | Area (ha) |
| | | Edge (m) |
| | Shape metrics | Perimeter–area ratio<br>Shape index<br>Fractal dimension |
| | Aggregation metrics | Euclidean nearest neighbour distance (m) |
| | | Proximity index |

Finally, a Kruskal–Wallis test was performed on SPSS Statistics v.27 software to check for significant differences between patch metrics for the three moments. The Kruskal–Wallis test is a nonparametric method for testing if multiple groups follow the same distribution. Next, a post hoc Dunn's test was used for pairwise comparisons, in the case of rejection in the Kruskal–Wallis test, to identify which date shows a significant difference. These results were then interpreted considering the landscape as a whole and for each individual land cover class and thus are presented together with the landscape- and class-level analyses.

## 3. Results

### *3.1. Land Cover*

Between 1947 and 2019, the city of Porto experienced an overall trend of an increase in artificial areas, at the expense of vegetated areas (Figures 3 and 4). In 1947, the municipality of Porto exhibited two key urban areas, represented here as agglomerations of the land cover class of Artificial Built Elements (ABE): a smaller one, in the southwest, near the estuary of Douro River, and the main urban core, in a more central-southern position. These built-up areas have greatly expanded throughout the years, resulting in the duplication of the urban surface (from 31% in 1947 to 62% in 2019), currently forming an almost continuous mesh. The stability in the number of patches of ABE, along with the substantial increase in the proportion of the landscape (Figure 3), indicates that no new separate urban areas were created, but rather the existing ones were enlarged.

Large patches of arboreal vegetation exist mainly in the peripheral areas of Porto, especially in the western and eastern extremes, with most of them being preserved since the mid-20th century (Figure 4). This caused the percentage of woody vegetation (TRS) within the city, as well as the number of patches, to remain virtually unchanged from 1947 to 2019 (between 22% and 25% cover, and between 750 and 783 patches; Figure 3). On the other hand, the city has experienced a drastic change in the proportion of herbaceous cover (HER): in 1947, the landscape was clearly dominated by herbaceous vegetation, with approximately 40% cover, which reduced to 10% in 2019 (Figures 3 and 4). Through visual analysis of the land cover maps, but mainly by means of the interpretation of the increase in the number of patches, accompanied by the reduction in the percentage cover, it becomes clear that herbaceous habitats were the most affected in terms of availability and connectivity.

Although the classes of Sparsely Vegetated—Terrestrial (SPV) and Sparsely Vegetated—Aquatic (AQU) are considered as components of ecologically significant habitats, they have remained consistent through the time period 1947–2019 and are residual in this study area (always less than 5%; Figure 3). Thus, SPV and AQU will not be analysed in detail as they play a reduced role in the interpretation of land cover evolution in the city of Porto.

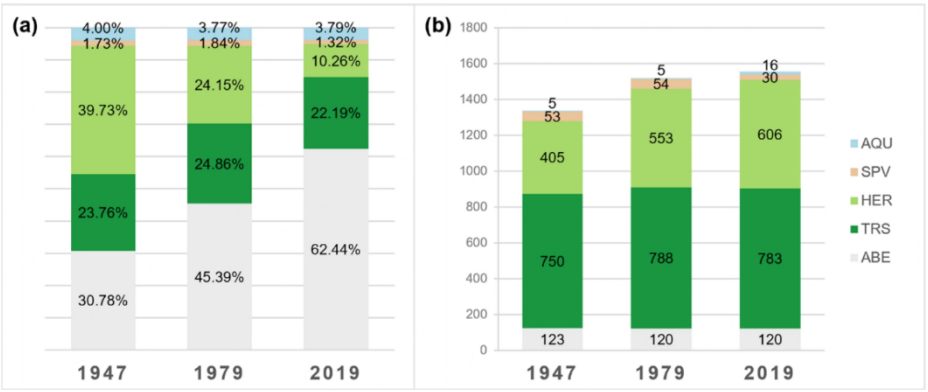



**Figure 3.** (**a**) Land cover class proportions in 1947, 1979, and 2019; (**b**) number of patches per class in 1947, 1979, and 2019 (see also Table A1).

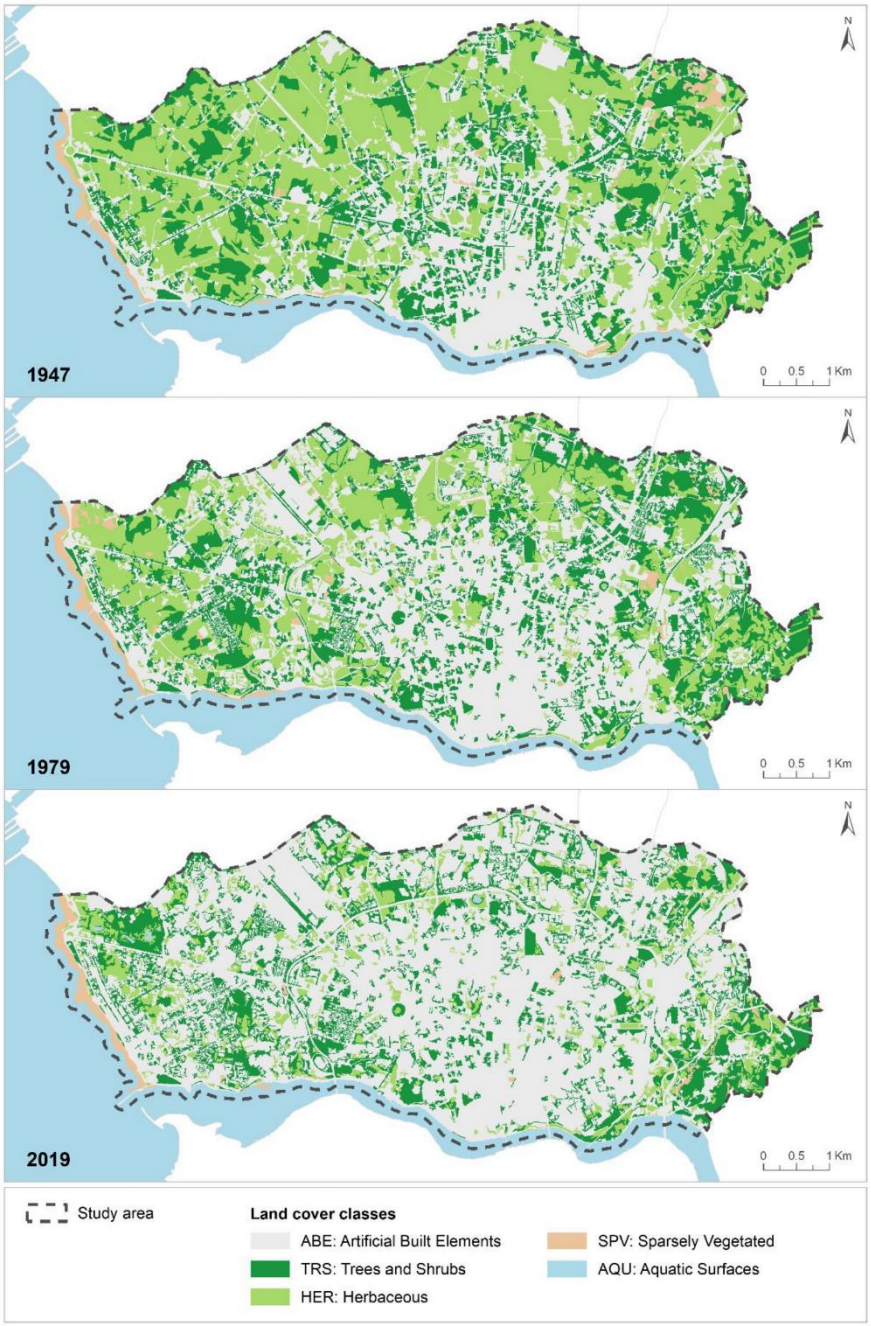



**Figure 4.** Land cover maps of Porto in 1947, 1979, and 2019.

### 3.2. Spatial Metrics

#### 3.2.1. Landscape-Level Analysis

At the landscape level, the overall perspective of spatial metrics seems to point to a general trend of increased complexity and fragmentation (Figure 5; see also Table A1). Although the analysed study area remains the same for every year, the number of patches (NP) has increased over time, resulting in the decline of mean patch size (MPS). The increase in mean patch edge (MPE) and edge density (ED), as well as in all shape metrics (mean perimeter–area ratio: MPAR, mean shape index: MSI, and mean fractal dimension: MFD), reveal a general increase in patch shape irregularity and intricacy.

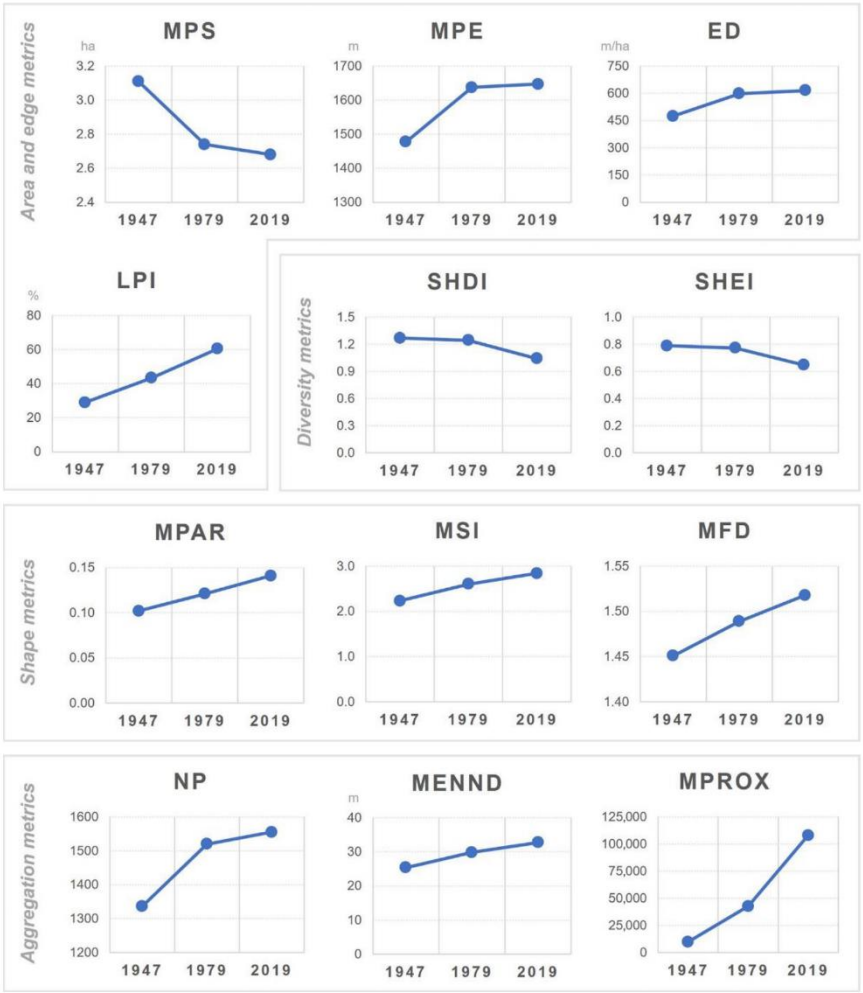



**Figure 5.** Evolution of spatial metrics at the landscape level, for the period 1947–1979–2019 (see Table A1 for detailed values). MPS: mean patch size; MPE: mean patch edge; ED: edge density; LPI: largest patch index; SHDI: Shannon's diversity index; SHEI: Shannon's evenness index; MPAR: mean perimeter–area ratio; MSI: mean shape index; MFD: mean fractal dimension; NP: number of patches; MENND: mean Euclidean nearest neighbour distance; MPROX: mean proximity index.

The values of mean Euclidean nearest neighbour distance (MENND) have increased throughout the analysed period, pointing to increased fragmentation and isolation of patches. Conversely, the values of mean proximity index (MPROX) have largely increased, suggesting higher proximity to large patches of the same land cover class. These results should be examined in more detail for a clearer interpretation (see class-level results below).

The territory seems to have experienced a decline in the diversity of land cover classes, especially during the transition from 1979 to 2019, as exposed by the decreasing values of the Shannon diversity index (SHDI) and the Shannon evenness index (SHEI). This indicates that one or more classes have become increasingly dominant over other classes, which can be better understood in the class-level analysis below.

Considering individual patch metrics, analysed for the entire landscape, the Kruskal–Wallis test revealed that most metrics showed significant differences for at least one of the periods; however, the mean values for Euclidean nearest neighbour distance did not differ significantly throughout the years (Table 3).

**Table 3.** Outputs of the Kruskal–Wallis test (and post hoc pairwise comparisons) on patch metrics, considering the analysis at the landscape level (N = 4411; significance values for Dunn's test were adjusted by the Bonferroni correction for multiple tests).

| Patch Metrics | Kruskal–Wallis Test | | | Dunn's Test | |
|---|---|---|---|---|---|
| | Test Statistic | d.f. | Sig. | Pairwise Comparisons | Adj. Sig. |
| Area | 53.069 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | 0.052<br><0.001 *<br><0.001 * |
| Edge | 18.047 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | 0.001 *<br><0.001 *<br>1.000 |
| Perimeter–area ratio | 403.910 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Shape index | 251.829 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Fractal dimension | 467.654 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Euclidean nearest neighbour distance | 0.803 | 2 | 0.669 | (pairwise comparisons were not performed as the overall test does not show significant differences across samples) | |
| Proximity index | 59.716 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | 0.020<br><0.001 *<br><0.001 * |

* Significant differences.

### 3.2.2. Class-Level Analysis

The spatial metrics for each individual class provide an overall image of increasing dominance of built-up areas (Figure 6; see also Tables A2–A4). As previously explained, the results for SPV and AQU are not presented nor discussed, as their relevance in the land cover dynamics of the territory is negligible at this scale of analysis.

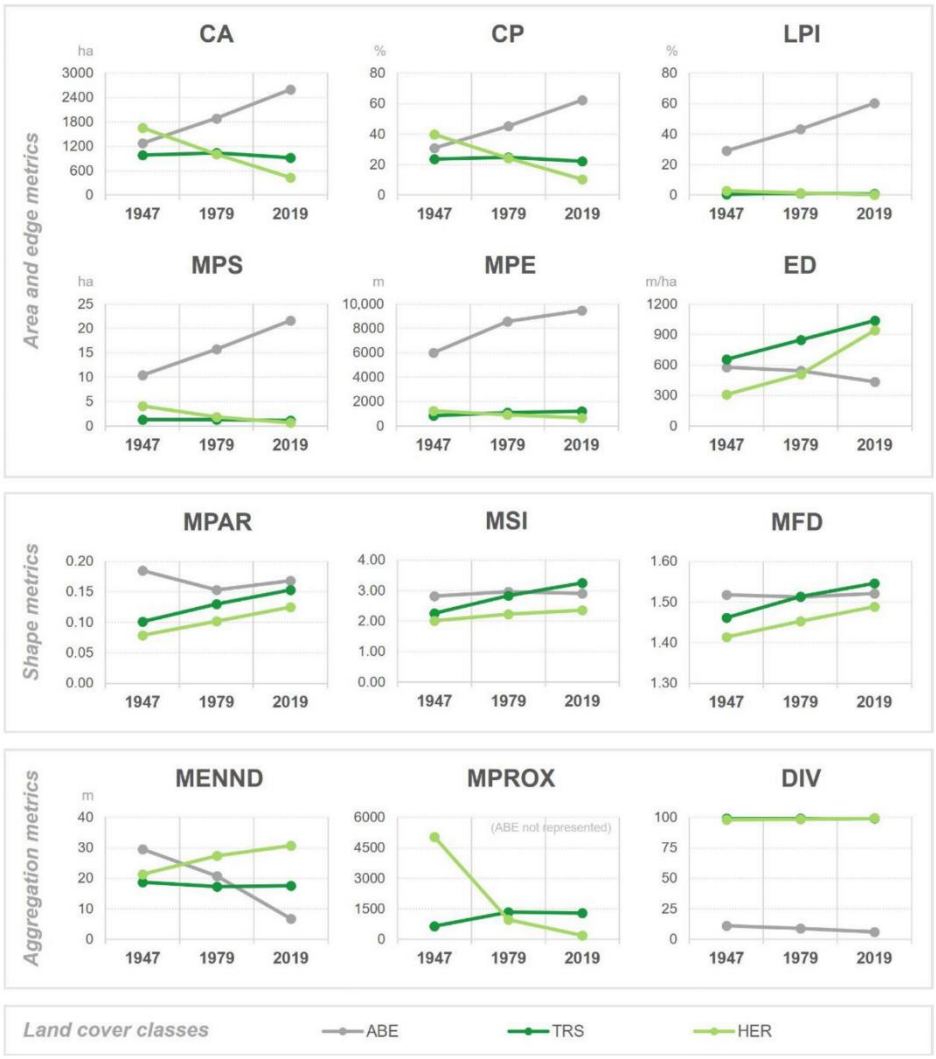



**Figure 6.** Evolution of spatial metrics at the class level, for the period 1947–1979–2019 (see Tables A2–A4 for detailed values). CA: total class area; CP: class proportion; LPI: largest patch index; MPS: mean patch size; MPE: mean patch edge; ED: edge density; MPAR: mean perimeter–area ratio; MSI: mean shape index; MFD: mean fractal dimension; MENND: mean Euclidean nearest neighbour distance; MPROX: mean proximity index; DIV: division index.

**Artificial Built Elements (ABE) cover.** As expected, following the global urbanisation trends of the 20th century, the class of ABE showed a substantial increment in area, as was revealed by the area metrics: class area (CA), class proportion (CP), largest patch index (LPI), mean patch size (MPS), and mean patch edge (MPE) gradually increase over time. Accordingly, the results in terms of aggregation metrics show a trend of decreasing MENND and increasing MPROX, which suggests higher connectivity among ABE patches over time. Shape complexity remained relatively constant throughout the years, as revealed by the evolution of shape metrics: MPAR, MSI, and MFD show similar values for the three time periods (Figure 6, Tables A2–A4). Regarding the analysis of individual patch

metrics for ABE land cover, the Kruskal–Wallis test revealed that most spatial metrics do not significantly differ in the three different moments, with the exception of Euclidean nearest neighbour distance and proximity index (Table 4).

**Table 4.** Outputs of the Kruskal–Wallis test (and post hoc pairwise comparisons) on patch metrics, considering the analysis for the ABE class (N = 363; significance values for Dunn's test were adjusted by the Bonferroni correction for multiple tests).

| Patch Metrics | Kruskal–Wallis Test | | | Dunn's Test | |
|---|---|---|---|---|---|
| | Test Statistic | d.f. | Sig. | Pairwise Comparisons | Adj. Sig. |
| Area | 1.019 | 2 | 0.601 | (pairwise comparisons were not performed) | |
| Edge | 3.734 | 2 | 0.155 | (pairwise comparisons were not performed) | |
| Perimeter–area ratio | 1.763 | 2 | 0.414 | (pairwise comparisons were not performed) | |
| Shape index | 1.933 | 2 | 0.380 | (pairwise comparisons were not performed) | |
| Fractal dimension | 2.426 | 2 | 0.297 | (pairwise comparisons were not performed) | |
| Euclidean nearest neighbour distance | 94.703 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | 0.001 *<br><0.001 *<br><0.001 * |
| Proximity index | 120.750 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |

* Significant differences.

**Herbaceous (HER) cover.** Area metrics (CA, CP, LPI, MPS, and MPE) reveal a severe decrease in the availability of HER land cover, while the increasing values of ED, as well as MPAR, MSI, and MFD, seem to point to a situation of increased patch shape complexity and irregularity over time. The evolution of aggregation metrics also suggests a rise in isolation and fragmentation of HER patches, as can be especially seen in the results of increasing values of MENND and decreasing values of MPROX (Figure 6, Tables A2–A4). According to the Kruskal–Wallis test, all patch metrics for HER land cover class show significant differences between the analysed time periods (Table 5).

**Trees and Shrubs (TRS) cover.** According to most area metrics (CA, CP, LPI, MPS), the land cover dominated by TRS apparently maintained a fairly constant area throughout the years. The evolution of aggregation metrics (NP, MENND, MPROX, and division index, DIV) also suggests the higher stability of this land cover type regarding availability and connectivity. However, the increasing values of edge (MPE, ED) and shape metrics (MPAR, MSI, MFD) reveal a scenario of increased shape complexity and irregularity (Figure 6, Tables A2–A4). Indeed, the Kruskal–Wallis test revealed that patch size and edge have significantly different values for the three analysed years, in addition to patch shape metrics (perimeter–area ratio, shape index, and fractal dimension). On the other hand, aggregation metrics for TRS have not changed significantly throughout the years (Table 6).

**General overview.** When analysing the city at a broad scale, there is an obvious trend of urban sprawl and densification, but this was translated with different spatial patterns in distinct portions of the city. Four main tendencies of land cover evolution were identified throughout the city, which are represented in Figure 7: (i) dominance of ABE from at least 1947 to the present, mostly visible in the city centre; (ii) drastic urban expansion, especially from 1979 onward, with the consequent elimination of HER cover, particularly noticeable in the northern section; (iii) slight increase in ABE surface, but with consequences in terms of increased fragmentation and irregularity of TRS and HER cover, as can be seen, for example, in the western section; and (iv) decrease in HER cover associated with increase in TRS cover, also coupled with moderate increase in ABE, as occurred in the eastern area.

**Table 5.** Outputs of the Kruskal–Wallis test (and post hoc pairwise comparisons) on patch metrics, considering the analysis for the HER class (N = 1564; significance values for Dunn's test were adjusted by the Bonferroni correction for multiple tests).

| Patch Metrics | Kruskal–Wallis Test | | | Dunn's Test | |
|---|---|---|---|---|---|
| | Test Statistic | d.f. | Sig. | Pairwise Comparisons | Adj. Sig. |
| Area | 87.608 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Edge | 6.621 | 2 | 0.036 * | 1947–1979<br>1947–2019<br>1979–2019 | 1.000<br>0.044 *<br>0.212 |
| Perimeter–area ratio | 236.792 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Shape index | 63.766 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Fractal dimension | 221.490 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Euclidean nearest neighbour distance | 33.985 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | 0.028 *<br><0.001 *<br>0.002 * |
| Proximity index | 59.716 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | 0.020<br><0.001 *<br><0.001 * |

* Significant differences.

**Table 6.** Outputs of the Kruskal–Wallis test (and post hoc pairwise comparisons) on patch metrics, considering the analysis for the TRS class (N = 2321; significance values for Dunn's test were adjusted by the Bonferroni correction for multiple tests).

| Patch Metrics | Kruskal–Wallis Test | | | Dunn's Test | |
|---|---|---|---|---|---|
| | Test Statistic | d.f. | Sig. | Pairwise Comparisons | Adj. Sig. |
| Area | 8.280 | 2 | 0.016 * | 1947–1979<br>1947–2019<br>1979–2019 | 0.486 *<br>0.012 *<br>0.402 * |
| Edge | 56.523 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br>0.017 * |
| Perimeter–area ratio | 319.709 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Shape index | 302.895 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Fractal dimension | 452.896 | 2 | <0.001 * | 1947–1979<br>1947–2019<br>1979–2019 | <0.001 *<br><0.001 *<br><0.001 * |
| Euclidean nearest neighbour distance | 4.508 | 2 | 0.105 | (pairwise comparisons were not performed) | |
| Proximity index | 0.924 | 2 | 0.630 | (pairwise comparisons were not performed) | |

* Significant differences.

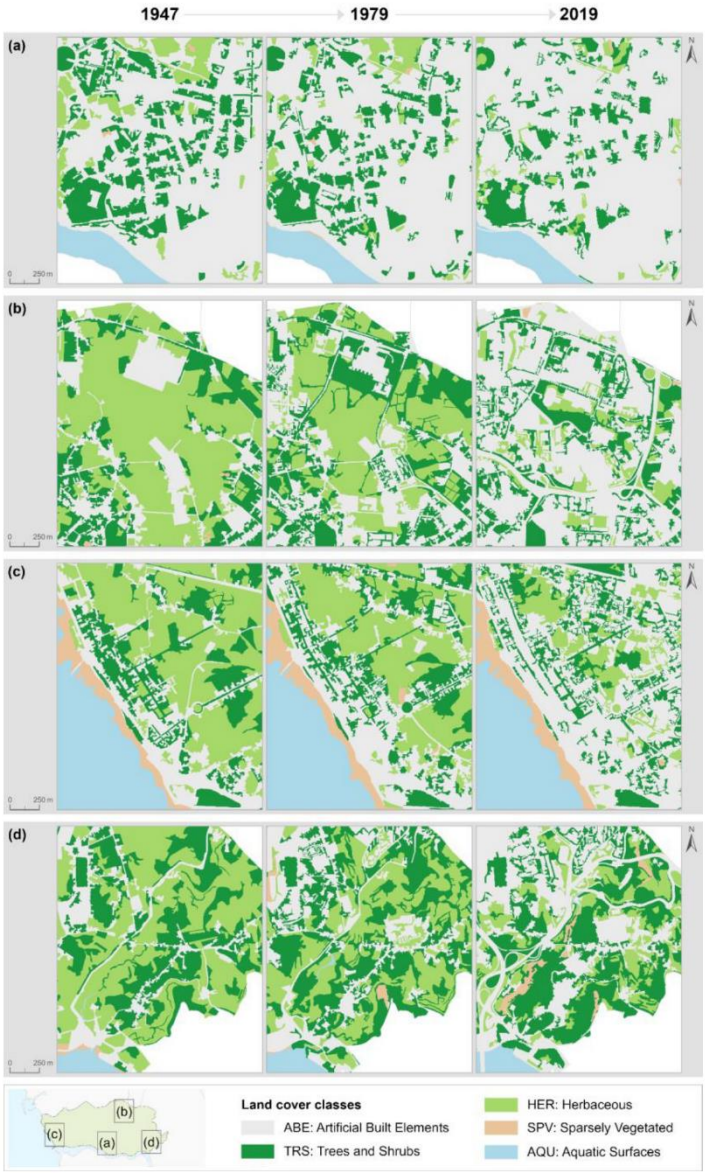



**Figure 7.** Different sections of the city, showing the main tendencies of land cover evolution: (**a**) section of the city near the centre, where ABE cover has been dominant since at least 1947; (**b**) section of the city near the northern border, that faced a significant increase in ABE cover and decrease in HER cover; (**c**) section of the city in the western extremity, where the increase in ABE cover resulted in the reduction and fragmentation of HER and TRS cover; (**d**) section of the city near the eastern limit, where HER cover was replaced by TRS and ABE cover.

## 4. Discussion

The city of Porto epitomises many of the urbanisation trends in vegetation cover observed in many European cities, having experienced a notorious sprawl and densification of its urban fabric in the past few decades [9,54,55]. In the first half of the 20th century, its

territory encompassed a small city centre, as well as a few ramifications to even smaller urbanised clusters in the periphery, and was still being dominated by vegetation cover, especially herbaceous vegetation in agricultural fields. The second half of the 20th century saw an acceleration of urbanisation, and at the beginning of the 21st century, the urban fabric occupied most of the territory contained by the boundaries of Porto. The former rural areas that surrounded the historical urban centres were progressively conquered by new urbanisation processes, which caused the increased dominance of buildings and sealed surfaces (ABE cover), as well as the reduction in diversity of land cover types. Most of the herbaceous patches (HER cover) have disappeared or have been extremely fragmented and isolated from similar patches; this is mainly due to the reclamation of land for new urbanisation, but also related to the abandonment of agricultural practices. Nowadays, most of the remaining vegetation cover persists in patches of trees (TRS cover), which reveals some concern with the preservation of tree cover; in fact, while some new tree cover originated from the ecological succession in abandoned or unmanaged lots, most of the larger tree-covered patches that existed in the mid-20th century were integrated in new public parks.

These results are in line with previous studies performed for the Porto region, although for different contexts, time frames, and scales of approach. For example, in their analysis of the evolution of green spaces in Porto in the 20th century, Madureira et al. [56] demonstrated a severe decrease in agricultural areas, accompanied by a general increase in green space destruction and fragmentation. Similarly, Bagan and Yamagata [57] revealed an association between the urban growth of Porto and the reduction in several types of vegetation cover, within a shorter, more recent period, from 1984 to 2009. Several other cities, in Europe and worldwide, also present an urbanisation scenario similar to that experienced by Porto in the past few decades: an increase in built-up and impervious areas and a decline in vegetation and green space cover (e.g., [9,58–60]); however, it should be noted that most of these studies consider only short-term changes, rarely encompassing more than 20 or 30 years of urban land cover evolution. With a similar time frame to our study, Lennert et al. [61] explored the past dynamics of the Budapest metropolitan region from 1959 to 2012 and obtained similar results: the growth in artificial surfaces caused the decline in vegetated areas, such as natural or agricultural land; nevertheless, the large-scale approach can make it difficult to translate to local actions in each of the individual municipalities. It is worth mentioning that a lot of cities, especially large European and North American cities, have been able to counteract this tendency of vegetation cover loss since the late 20th century [9,62]. While some of these trends can be explained by the rise in temperatures favouring vegetation growth, many of these cities have in fact strengthened their green infrastructure and promoted the application of nature-based solutions [63]. This could also be the case of Porto if the outcomes of this study are properly integrated in urban planning.

The fine scale of analysis allows for a detailed look at specific portions of the city, which can be particularly relevant to understand the context and implications of future interventions in urban areas, which may be of significant interest for urban planners and decision makers. For example, the city centre (Figure 7a) has been dominated by ABE for a long time, with a fairly constant area, and TRS cover also seems to be quite persistent. This may be suggestive of some habitat and green space conservation efforts, as most of the TRS patches that were already present in 1947 belonged to public parks, gardens, or green squares that were maintained to the present day; some private green spaces inside blocks of buildings have also been preserved. Thus, it is essential that, in this densely built area, all pervious land is protected from future construction and new opportunities for the increment of vegetation cover are seized and planned carefully to maintain appropriate levels of vegetation diversity.

On the other hand, the northern part of Porto (Figure 7b) reveals an obvious scenario of rapid urban expansion where agricultural fields, dominated by HER cover, were progressively displaced by urbanisation, seemingly without much planning or conservation concerns. In this section of the city, the loss and fragmentation of vegetated areas become

quite noticeable, especially due to large continuous patches of HER cover, and also TRS cover to a lesser extent, being encroached by the development of new buildings, roads, and other infrastructures (ABE). It is recommended that future interventions in this or other areas with a similar profile take actions to preserve, enlarge, and connect the remnant patches of vegetation, in order to enhance the ecological performance of the urban ecosystem.

The western extreme of the city (Figure 7c) also shows a significant decrease in the proportion of HER cover due to the decline in agricultural activities. The scenario of increase in fragmentation and shape irregularity of TRS cover is particularly visible in this portion of the city, as large patches of tree-covered private gardens and backyards, present in 1947, were gradually replaced by a denser matrix of buildings; most of the TRS patches in 2019 are tree-lined streets and narrow fragments of private gardens. In this area of the city, there are still some relatively large patches dominated by herbaceous vegetation that represent some of the few cultivated areas in the whole city that persist today. Considering the future urban developments expected for this area, we recommend that this portion of land retains the highest degree of perviousness as possible, protecting one of the few areas of the city with less disturbed soil. In this regard, we highlight two major options: (1) the preservation of agricultural spaces, for example, in the form of community gardens or allotments, and (2) the establishment of herbaceous habitats, based mainly on native plant species. These practices could contribute to the conservation of soil and water quality, while also promoting the biodiversity of grassland and farmland habitats, which is declining at the European level [64].

The eastern portion of Porto (Figure 7d) was also dominated by HER cover in 1947, mainly in the form of crops and pastures. Although some new urban developments occurred, namely the construction of a few residential neighbourhoods and large roads, this portion remains one of the least urbanised of the city. However, the area of HER cover has also decreased substantially, especially due to the abandonment of agricultural fields, which caused an increment in mostly spontaneous TRS cover. This can pose an additional challenge due to the proliferation of invasive species that may follow the abandonment of these fields. Nevertheless, the extent of vacant land present in this portion of the city can generate opportunities for the creation of new accessible green spaces that provide numerous benefits for the urban population, especially considering the lack of public green spaces amongst this intricate urban fabric with an accentuated rural character.

Due to their higher degree of complexity and heterogeneity, the smaller scale of approach seems to be particularly relevant in urban areas, where there is a strong competition for space among different interest groups and where decisions at a small scale can have significant ecological or social effects. For instance, decisions such as the preservation of even a small patch of vegetation can dictate the survival of a population of a certain species or can contribute to the experience of nature for the nearest residents, improving their health, well-being, and quality of life at a scale that even transcends that particular site.

To complement these results, further data could be generated encompassing, for example, a more detailed classification of vegetation types, a finer temporal scale (considering shorter time intervals), and the study of land cover trajectories. Additionally, depending on the aim of research, but particularly relevant for spatial planning, it may be worth analysing the relationship between land cover patterns and evolution with biodiversity, quality of life, health and well-being, and other factors.

As such, this research can be easily reproduced in a variety of urban areas, as the methods are quite simple and do not require prior specialised training for the visual interpretation of the landscape. However, due to the detailed scale of analysis, the method can become quite time-consuming when considering larger study areas; this could be overcome with the creation of automatic algorithms for the classification of land cover, which was outside of the scope of this research.

## 5. Conclusions

The city of Porto experienced evident processes of urban sprawl and densification in the last century, mimicking other cities worldwide. Thus, the findings and recommendations of this research can also be applied to a variety of cities with a similar context, particularly other European cities that are compact and undergoing phases of infill development. To counteract the loss of vegetation, especially grassland and farmland habitats, we propose that these cities invest in the conservation, restauration, or creation of herbaceous patches, in the form of meadows, allotments, urban farming, and other amenities, that could be encouraged in public and private areas. Arboreal vegetation is also important, but its conservation is a more common practice (that should be maintained). Cities that aim to be sustainable should consider several aspects regarding green spaces: maximise, to the greatest possible extent, the amount of vegetation cover in the city; enhance the diversity of green spaces and in green spaces (e.g., include different types of green spaces, with different uses and different compositions); optimise the relation of vegetation patches with each other and with the surrounding built environment; and consider the temporal variation or continuity of vegetation.

The small-scale approach of this research brings the results closer to the scale of intervention, i.e., it allows a focus, with great detail, on particular sites, contributing to decision making in future interventions in the urban landscape (e.g., preservation of the existing vegetation, selection of the best habitats to implement, etc.). This way, the scale of approach and the emphasis on vegetation facilitate the translation of scientific research into concrete practical measures, and not just general recommendations on a broad geographic scale that are difficult to implement at the local decision scale.

This study showed that it is possible to obtain urban land cover data at a fine spatial scale, while also considering the history of the vegetation on each location. This research was outlined with urban ecology and urban planning in mind, but it can also be useful to other fields of scientific research and professional practices, such as architecture, landscape architecture, geography, social studies, etc., that take interest in improving the urban environment and the health and quality of life for urban residents.

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## Appendix A. Values of Spatial Metrics

**Table A1.** Spatial metrics at the landscape level, for 1947, 1979, and 2019.

| Type | Metric | 1947 | 1979 | 2019 |
|---|---|---|---|---|
| Area and edge metrics | TA: Total area (ha) | 4160.75 | 4160.75 | 4160.75 |
| | LPI: Largest patch index (%) | 29.02 | 43.33 | 60.45 |
| | MPS: Mean patch size (ha) | 3.11 | 2.74 | 2.68 |
| | MPE: Mean patch edge (m) | 1477.24 | 1637.28 | 1646.62 |
| | ED: Edge density (m/ha) | 474.33 | 598.13 | 615.39 |
| Shape metrics | MPAR: Mean perimeter–area ratio | 0.102 | 0.121 | 0.141 |
| | MSI: Mean shape index | 2.235 | 2.604 | 2.844 |
| | MFD: Mean fractal dimension | 1.451 | 1.489 | 1.518 |
| Aggregation metrics | NP: Number of patches | 1336 | 1520 | 1555 |
| | MENND: Mean Euclidean nearest neighbour distance (m) | 25.40 | 29.84 | 32.78 |
| | MPROX: Mean proximity index | 9948.18 | 42,631.88 | 107,968.34 |
| Diversity metrics | CR: Class richness | 5 | 5 | 5 |
| | SHDI: Shannon's diversity index | 1.270 | 1.245 | 1.043 |
| | SHEI: Shannon's evenness index | 0.789 | 0.773 | 0.648 |

**Table A2.** Area and edge metrics at the class level, for 1947, 1979, and 2019.

| Metric | Class | 1947 | 1979 | 2019 |
|---|---|---|---|---|
| CA: Total class area (ha) | ABE | 1280.83 | 1888.41 | 2597.82 |
| | TRS | 988.49 | 1034.21 | 923.29 |
| | HER | 1653.23 | 1004.87 | 427.03 |
| | SPV | 71.84 | 76.50 | 54.89 |
| | AQU | 166.35 | 156.75 | 157.71 |
| CP: Class proportion (%) | ABE | 30.78 | 45.39 | 62.44 |
| | TRS | 23.76 | 24.86 | 22.19 |
| | HER | 39.73 | 24.15 | 10.26 |
| | SPV | 1.73 | 1.84 | 1.32 |
| | AQU | 4.00 | 3.77 | 3.79 |
| LPI: Largest patch index (%) | ABE | 29.02 | 43.33 | 60.45 |
| | TRS | 0.66 | 1.03 | 0.93 |
| | HER | 2.82 | 1.43 | 0.22 |
| | SPV | 0.45 | 0.49 | 0.92 |
| | AQU | 3.16 | 2.22 | 2.10 |
| MPS: Mean patch size (ha) | ABE | 10.41 | 15.74 | 21.65 |
| | TRS | 1.32 | 1.31 | 1.18 |
| | HER | 4.08 | 1.82 | 0.70 |
| | SPV | 1.36 | 1.42 | 1.83 |
| | AQU | 33.27 | 31.35 | 9.86 |
| MPE: Mean patch edge (m) | ABE | 6015.93 | 8559.07 | 9474.38 |
| | TRS | 863.69 | 1111.26 | 1223.57 |
| | HER | 1264.95 | 923.00 | 665.25 |
| | SPV | 767.90 | 801.37 | 830.30 |
| | AQU | 6570.87 | 6441.96 | 2341.89 |
| ED: Edge density (m/ha) | ABE | 577.72 | 543.89 | 437.65 |
| | TRS | 655.31 | 846.71 | 1037.65 |
| | HER | 309.88 | 507.94 | 944.06 |
| | SPV | 566.52 | 565.67 | 453.80 |
| | AQU | 197.50 | 205.49 | 237.59 |

**Table A3.** Shape metrics at the class level, for 1947, 1979, and 2019.

| Metric | Class | 1947 | 1979 | 2019 |
|---|---|---|---|---|
| MPAR: Mean perimeter–area ratio | ABE | 0.185 | 0.153 | 0.168 |
| | TRS | 0.101 | 0.130 | 0.153 |
| | HER | 0.079 | 0.102 | 0.125 |
| | SPV | 0.096 | 0.109 | 0.098 |
| | AQU | 0.126 | 0.046 | 0.066 |
| MSI: Mean shape index | ABE | 2.817 | 2.965 | 2.909 |
| | TRS | 2.263 | 2.829 | 3.259 |
| | HER | 2.010 | 2.235 | 2.361 |
| | SPV | 2.055 | 2.222 | 1.915 |
| | AQU | 3.760 | 3.247 | 2.071 |
| MFD: Mean fractal dimension | ABE | 1.518 | 1.512 | 1.521 |
| | TRS | 1.461 | 1.513 | 1.546 |
| | HER | 1.414 | 1.453 | 1.489 |
| | SPV | 1.439 | 1.459 | 1.436 |
| | AQU | 1.501 | 1.416 | 1.389 |

**Table A4.** Aggregation metrics at the class level, for 1947, 1979, and 2019.

| Metric | Class | 1947 | 1979 | 2019 |
|---|---|---|---|---|
| NP: Number of patches | ABE | 123 | 120 | 120 |
| | TRS | 750 | 788 | 783 |
| | HER | 405 | 553 | 606 |
| | SPV | 53 | 54 | 30 |
| | AQU | 5 | 5 | 16 |
| MENND: Mean Euclidean nearest neighbour distance (m) | ABE | 29.51 | 20.73 | 6.71 |
| | TRS | 18.73 | 17.36 | 17.63 |
| | HER | 21.30 | 27.47 | 30.72 |
| | SPV | 126.96 | 247.82 | 408.95 |
| | AQU | 181.13 | 123.33 | 342.81 |
| MPROX: Mean proximity index (*for a 100 m buffer*) | ABE | 87,302.27 | 526,604.25 | 1,389,437.08 |
| | TRS | 647.79 | 1340.99 | 1299.65 |
| | HER | 5036.90 | 964.48 | 201.06 |
| | SPV | 161.31 | 69.81 | 187.65 |
| | AQU | 3650.34 | 2822.40 | 826.43 |
| DIV: Division index | ABE | 11.10 | 8.85 | 6.24 |
| | TRS | 99.37 | 99.19 | 99.23 |
| | HER | 97.95 | 98.64 | 99.59 |
| | SPV | 89.01 | 88.26 | 50.54 |
| | AQU | 35.13 | 59.05 | 64.32 |

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**Article II**

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# Assessment of land cover trajectories as an indicator of urban habitat temporal continuity

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## HIGHLIGHTS

- Fast and simple method to identify priority urban habitats for conservation.
- The vegetation cover in Porto was significantly reduced from 1947 to 2019.
- Wooded habitats have persisted mainly in public parks and gardens.
- Herbaceous habitats are rare and extremely susceptible to new urban development.
- We propose the preservation, restoration, and expansion of stable habitats.

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## ABSTRACT

The trends of land cover dynamics in cities have major repercussions on urban biodiversity, ultimately impacting the health and well-being of human urbanites. Older habitats, i.e., habitats with higher spatiotemporal continuity, allow ecosystem processes promoting the maintenance of diverse microhabitats and the accommodation of diverse species over time, contributing for a richer biodiversity at the city level and beyond. Thus, we implement the analysis of land cover trajectories proposed as an indicator of habitat continuity, in order to identify priority areas for conservation or restoration that can be integrated in urban planning. The method was applied in the city of Porto, Portugal, and it was used to detect the main habitat patches associated with trends of vegetation persistence, gain and loss, between 1947 and 2019. The most common change was related to urbanization processes, where artificial built elements replaced areas of tree, shrub and herbaceous cover, completely dominating the territory in 2019 (66% cover). Moreover, tree and shrub cover had a relatively balanced dynamics, keeping a constant area (20–25%) while newly created wooded habitats compensated for the lost ones. Finally, areas covered with herbaceous vegetation suffered a drastic loss and fragmentation over the period of 72 years (from 40% in 1947 to 10% in 2019). This analysis of land cover evolution allowed for the identification of areas that have been continuously covered by vegetation, displaying a greater stability and higher probability of habitat continuity. This information, with its spatially explicit character, can help to inform future planning, design and management policies at a local scale and contribute to the conservation, restoration and expansion of urban habitats and their biodiversity.

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## 1. Introduction

Habitat loss and transformation is one of the major threats to biodiversity and urbanization is one of the main culprits (McKinney, 2002; Simkin et al., 2022; Tilman et al., 2017). Human populations are frequently settled in areas with rich soils and vegetation, often near waterbodies, which can exhibit high levels of biodiversity (Chapman & Underwood, 2009; Ives et al., 2016; Kowarik, 2011). However, urbanization causes the destruction, degradation, fragmentation and isolation of natural habitats, alteration of natural disturbance regimes and introduction of non-native species (Gaertner et al., 2017; Kowarik, 2011). On the other hand, urbanization is responsible for the emergence of new habitats in these areas, creating a diverse mosaic of semi-natural and man-made habitats, home to unique assemblies of flora and fauna species (Müller et al., 2013; Spotswood et al., 2021).

Urban biodiversity is crucial for ecosystem functioning (Harrison et al., 2014; Millennium Ecosystem Assessment, 2005; Zari, 2018) and it is beneficial to the health, well-being, and quality of life of urban residents (Aerts et al., 2018; Schebella et al., 2019). Preservation and promotion of urban biodiversity is fundamental if cities want to tackle climate challenges and achieve sustainability (Huang et al., 2018; Xie & Bulkeley, 2020). As such, it is thus essential that urban planning and landscape design integrate actionable ecological knowledge (Garrard et al., 2018; Zhou et al., 2019), ideally including spatially explicit data and at the appropriate spatial and temporal scales (Aronson et al., 2017; Borgström et al., 2006; Jarvis & Young, 2005; Opdam et al., 2013). With urban biodiversity conservation in mind, planners and decision makers must plan for the availability of relevant habitats, specific to each geographic context. In addition to the creation of new urban green spaces, it is imperative to preserve the oldest habitats (Kowarik & von der Lippe, 2018; McKinney, 2002). While newly created habitats can show high species richness, they are commonly occupied by non-native species and generalist native species that can tolerate a diverse range of conditions and disturbance (Callaghan et al., 2019; Ducatez et al., 2018). If habitat quality is maintained, habitat continuity (i.e. the persistence of a particular habitat type through time) supports the occurrence of specialist species in these old habitats (Lõhmus & Liira, 2013; Nordén et al., 2014; Raduła et al., 2020) and consequently promotes a higher species diversity at the city level.

However, despite the call for action of international experts and institutions (e.g. ICLEI, 2020; Secretariat of the Convention on Biological Diversity, 2012), many cities face multiple challenges to manage and preserve their biodiversity (Cooper et al., 2021; Wilkinson et al., 2013). In this context, there is still a lack of ecological knowledge on the functioning of the urban ecosystem and, frequently, the available data is inadequate to meet the requirements of urban planners, designers and managers (Jarvis & Young, 2005; Zhou et al., 2019), especially at the local level (McDonnell & Hahs, 2013; Wilkinson et al., 2013). Remarkably, this is the level where planning and management decisions directly translate into site interventions that modify urban habitats (Brown, 2017; Opdam et al., 2013). There is often a disconnection between the spatial and temporal scale of ecological information and the practices and policies that influence the urban environment (Borgström et al., 2006; Opdam et al., 2013; Uchida et al., 2021), which makes it difficult to integrate scientific data in spatial planning and urban habitat conservation programs (Brown, 2017; Łopucki & Kiersztyn, 2015; Opdam et al., 2013). Spatialization of ecological data is considered a fundamental tool to improve the communication between multidisciplinary scientific teams and non-expert decision-makers and to contribute to generate knowledge that is useful to inform urban planning, design and management (Jarvis & Young, 2005; Pedersen et al., 2004).

Habitat availability (in space and time) is an important determinant of species dynamics and several authors have highlighted the importance of its temporal aspect (Cadenasso et al., 2006; Hanski, 1999), particularly in urban ecosystems (Alberti et al., 2020; Müller et al., 2013; Ramalho & Hobbs, 2012). However, it is most common that in urban ecology studies, habitat availability is evaluated from a merely static perspective, which disregards the intrinsic dynamism of urban environments. Few urban ecological studies include the temporal component (Ossola et al., 2021); this can be assessed as patch continuity, habitat age, site history, or land-use legacy (e.g. Gustavsson et al., 2007; Johnson et al., 2018). The temporal aspect of habitat availability can influence the occurrence of diverse organisms over time through a multitude of processes. For example, it interferes with processes typically associated with metapopulation or metacommunity dynamics, such as dispersal, (re)colonization, and extinction, by causing time-lagged responses to landscape change, which in turn can cause a phenomenon of extinction debt or immigration (or species) credit (Lira et al., 2019; Swan et al., 2021; Uroy et al., 2021). Furthermore, habitats with higher continuity, i.e., those older and more stable, offer better conditions for specialist species, as these are often associated with habitat niches that take time to develop, such as tree cavities or wood decay (Janssen et al., 2017; Nordén et al., 2014).

In the scope of biodiversity conservation in an urban context, the following questions arise: Which, and where, are the areas that present a higher probability of habitat continuity in time? How can they be rapidly identified in a context of insufficient biodiversity data and low financial resources? In this regard, here we propose the analysis of land cover trajectories as an indicator of habitat continuity, in order to identify priority areas for conservation or restoration that can be integrated in urban planning. Using the city of Porto, in Portugal, as a case study, our research objectives were: 1) to determine and spatially represent the land cover trajectories from the mid-20th century to a recent date; 2) to assess the main changes in vegetation patches in terms of persistence, gain or loss; 3) to identify the habitat patches subject to a lesser degree of habitat disruption and, consequently, exhibiting a higher degree of continuity.

## 2. Methods

### 2.1. Study area

This study focuses on the Municipality of Porto, located in the northern region of Portugal (Fig. 1). Porto presents itself as a relatively small city (42 $km^2$, 232 000 inhabitants; INE, 2022), but it is the center of a dynamic metropolitan area comprised of 17 municipalities and around 1.7 million residents (AMP, 2022). Its privileged location at the intersection of the Douro River and the Atlantic Ocean and the mild temperate climate (*Csb* regime, Koppen-Geiger classification; Peel et al., 2007) conduced to a rich human history, as well as rich biodiversity levels (Guilherme et al., 2015).

### 2.2. Land cover trajectories

This study follows the work of Guilherme et al. (2022), which classified the land cover in Porto for the years 1947, 1979 and 2019, based on aerial photography and satellite imagery, using an adaptation of the UrHBA method (Farinha-Marques et al., 2017). UrHBA methodology is spatially explicit, based on the visual interpretation of the landscape and it excels at capturing urban habitat diversity at a fine scale. The mapping and classification of land cover was made in vectorial format in a GIS environment, with the older images being previously orthorectified (Guilherme et al., 2022). In a context of limited time and resources, and due to the limitations of historic remote sensing data, the mapping procedure was streamlined – all elements were mapped as patches, even if with a linear shape; the minimum dimension for patches to be distinguished was 2000 $m^2$, and the minimum width was 5 m. The classification was also simplified to five land cover categories: 1) Artificial Built Elements, ABE, 2) Trees and Shrubs, TRS, 3) Herbaceous, HER, 4) Sparsely Vegetated - Terrestrial, SPV, and 5) Sparsely Vegetated - Aquatic, AQU (see Guilherme et al., 2022 for more details). In an urban context, ABE consists of impervious surfaces and buildings; TRS

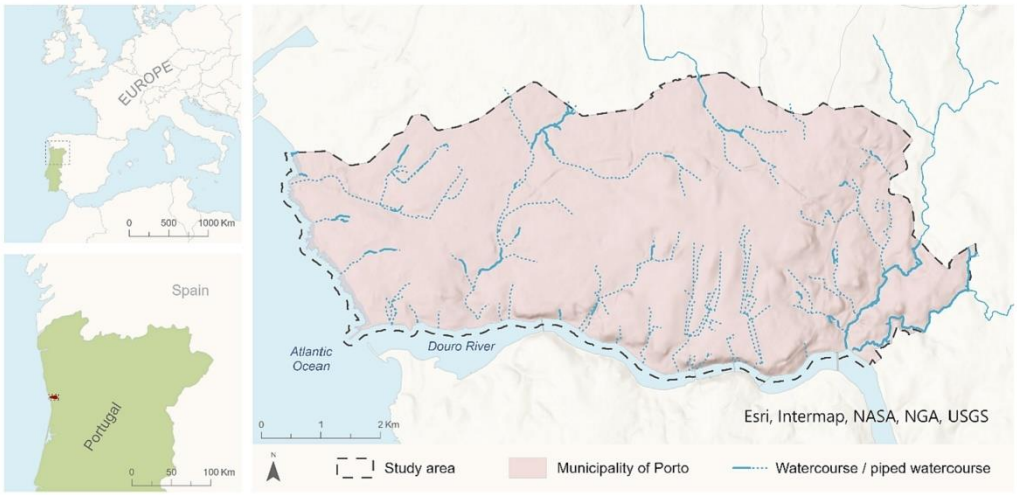



**Fig. 1.** Location of the study area, in northern Portugal.

identifies all tree and shrub cover, which can occur in parks, gardens, forested areas, scrub/bushland, riparian galleries, wooded crops, tree-lined streets, etc.; HER marks all areas covered by herbaceous vegetation, including both areas only temporarily covered with herbaceous vegetation and areas with frequent arrest to successional processes to maintain a permanent herbaceous cover, such as lawns, meadows, allotment or vegetable gardens, herbaceous crops, pastures, semi-natural grasslands, spontaneous vegetation in vacant lots, etc.; SPV consists of every type of non-vegetated soil, such as bare soil, sand, and rock; AQU comprises water surfaces, such as the sea, rivers, lakes, and ponds (including artificial water elements).

The method is based on the concept of land cover, which refers to the physical material that covers the surface of the land (Haines-Young, 2009; Jarvis & Young, 2005) and is easily applicable in a multitude of geographic contexts as it transcends local and cultural conditions (Farinha-Marques et al., 2017). It seems particularly relevant in urban ecological studies as it is associated with habitat types (Farinha-Marques et al., 2017) and it can be directly transformed through most urban interventions, not necessarily requiring a change in land use type (Haines-Young, 2009). At a fine scale, land use classification, being strongly associated with socio-economic activities, could fail to capture small habitat patches as the vegetation categories can occur in a variety of land use types; likewise, areas classified with the same land use type could encompass different vegetation covers.

Land cover trajectories are a common method to assess trends of landscape change over time, usually derived from satellite images or aerial photograph, at a particular location and at multiple dates (Gbanie et al., 2018; Liu & Cai, 2012). As such, the land cover layers for 1947, 1979 and 2019 (in vectorial format; Guilherme et al., 2022) were overlapped, using the "intersect" tool in ArcMap Desktop 10.5. This generated a new layer of information regarding the trajectory of land cover for the entire surface of the city. To reduce errors and/or biases and to simplify the data analysis, this process included the elimination of sliver polygons (smaller than 100 $m^2$), i.e., they were absorbed into larger adjoining polygons; this was achieved with the "eliminate" tool (ArcMap Desktop 10.5). In the newly created layer, each polygon is then described by a sequence of three land cover categories, i.e., a land cover trajectory, reflecting its evolution from 1947, to 1979 and to 2019, as illustrated in Fig. 2. The resulting data allowed for the analysis of the transition in land cover considering three different time intervals: 1) from 1947 to 1979; 2) from 1979 to 2019; and 3) the complete sequence from 1947, to 1979, then to 2019.

### 2.3. Changes in vegetation cover

Focusing particularly on vegetated areas, we analyzed in more detail the land cover transformations that occurred in the study area, for trajectories related to TRS cover, HER cover and general vegetation cover (combining both TRS and HER in the same analysis). The areas were classified according to the chronological occurrence of vegetation as follows: 1) persistent cover - present in 1947, 1979 and 2019; 2) gained cover - absent in 1947, but present in 2019; 3) disturbed cover - present in 1947 and 2019, but absent in 1979; 4) gained then lost cover - absent in 1947 and 2019, but present in 1979; 5) lost cover - present in 1947 and absent in 2019.

The analysis of vegetation evolution led to the identification of the areas with persistent vegetation cover, i.e., areas that were covered with vegetation in 1947, 1979, and 2019. The areas with persistent

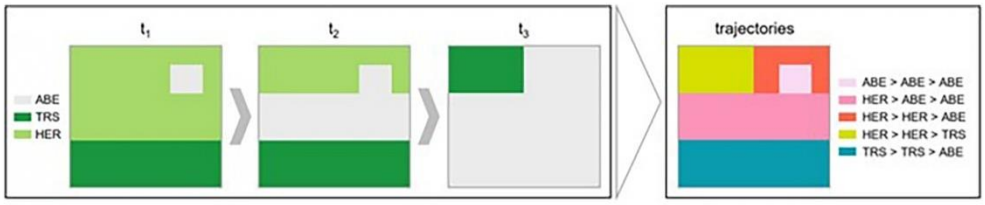



**Fig. 2.** Demonstrative example of the method for the classification of trajectories, using UrHBA categories in vectorial format.

vegetation were considered to have a higher probability of habitat continuity and, consequently, the areas with the most concentration of persistent vegetation were identified as the most important for habitat conservation and regeneration. Besides habitat continuity, these areas were also prioritized based on vulnerability to future land cover change, which was assessed based on their framing within urban planning instruments (Câmara Municipal do Porto, 2021a, 2021b), current land use, ownership, and accessibility. On one extreme, the areas with persistent vegetation that are included in environmental plans, that are currently integrated in green spaces, on the public domain, and publicly accessible, are considered the least vulnerable (and thus, the least priority). On the other extreme, the areas located in zones intended for urban development, that have no current use, are private domain, and are not publicly accessible, are considered the most vulnerable to habitat destruction and we consider they should be the top priority for conservation. For this purpose, vegetation patches located in public parks and gardens were considered to be the least susceptible to habitat destruction, as these areas tend to be preserved on the long term, since their conservation is usually included in urban plans and policies. Vegetation patches integrated on the green spaces of public and private services facilities (such as schools and hospitals) were classified as moderately susceptible, as these are relatively valued but are more prone to destruction when compared to public parks and gardens, as they are not included in environmental plans and policies. On the other hand, vegetation mainly located in undeveloped land or private green spaces was considered the most vulnerable to habitat loss, as these areas are frequently subject to urban pressure, being classified as areas destined to urban development.

## 3. Results

### 3.1. Land cover trajectories

The study of the dynamics of land cover transformation in Porto revealed 106 trajectories, amongst 125 possible ones, considering the set of five land cover categories. Of these trajectories, 11 stood out as predominant, covering in total more than 80% of the territory (Fig. 3). As an overall trend, derived by urbanization, over 62% of the study area has retained or acquired a higher degree of artificialization, i.e., marked by the coverage of Artificial Built Elements (ABE). Nevertheless, a considerable proportion of land has also maintained a less artificial land cover, namely Trees and Shrubs (TRS) and Herbaceous (HER), throughout the analyzed period of 72 years.

The city of Porto revealed a relatively dynamic land cover evolution, where almost 60% of the territory has experienced at least one change in its land cover since 1947 (Table 1). A smaller portion has been through

**Table 1**
Different situations of land cover dynamics and variation (and its distribution throughout the city).

| Land cover dynamics | Area (ha) | Proportion (%) | Land cover variation | Area (ha) | Proportion (%) |
|---|---|---|---|---|---|
| Land cover never changed | 1722.40 | 41.4% | Same land cover in 1947, 1979, and 2019 | 1722.40 | 41.4% |
| Land cover changed once | 1853.44 | 44.6% | Same land cover in 1947 and 1979 | 956.21 | 23.0% |
| | | | Same land cover in 1979 and 2019 | 897.23 | 21.6% |
| Land cover changed twice | 585.91 | 14.0% | Same land cover in 1947 and 2019 | 267.07 | 6.4% |
| | | | Different land cover in 1947, 1979, and 2019 | 318.84 | 7.6% |

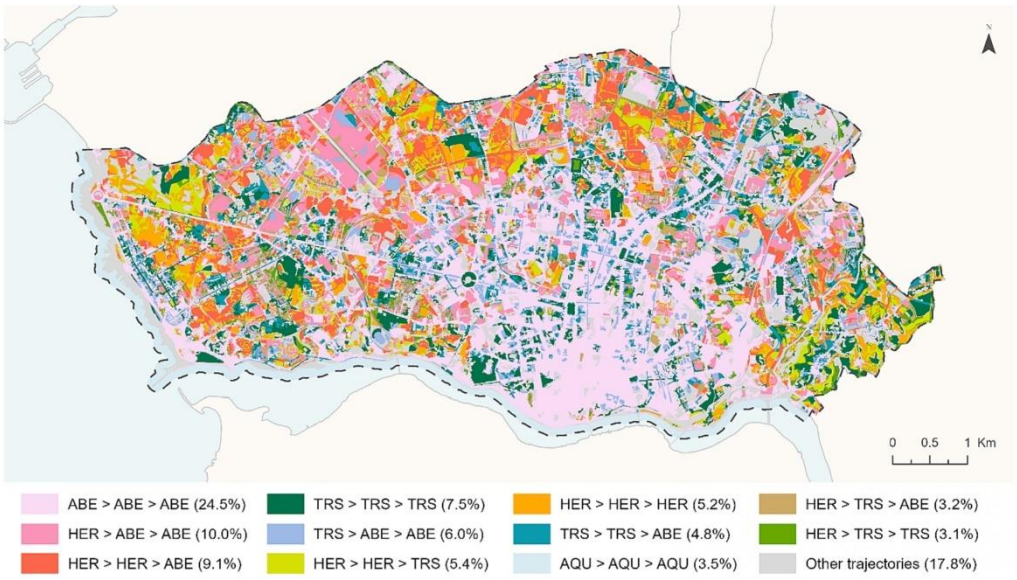



**Fig. 3.** Land cover trajectories from 1947, to 1979 and to 2019 (1947 > 1979 > 2019). Land cover categories: ABE, Artificial Built Elements; TRS, Trees and Shrubs; HER, Herbaceous; SPV, Sparsely Vegetated Terrestrial; AQU, Sparsely Vegetated Aquatic.

multiple transformations, with 7.6% of the study area exhibiting three different land cover for the three analyzed moments.

The city of Porto has experienced a marked increase in urbanization since the mid-20th century. From 1947 to 1979, the area covered by Artificial Built Elements (ABE) has increased by 47.7% (while maintaining 85.4% of their previous patches; Fig. 4); this growth was supported by the replacement of areas previously covered by herbaceous vegetation (HER, 494.60 ha), but also by trees and shrubs (TRS, 286.18 ha; Fig. 4; Table 2). From 1979 to 2019, the increment in ABE is also notorious; this time, ABE cover has incremented by 37.66%, while retaining almost 90% of previous areas. The destruction of vegetation patches continues to be the main source of land cover change, with 420.03 ha of TRS cover and 462.96 ha of HER cover being replaced by ABE cover (Fig. 4; Table 2). Artificial Built Elements (ABE) is the least dynamic category (besides AQU), since it retains almost all of the previous cover, experiencing mainly irreversible gains throughout the years (Fig. 4; Table 2). The most significant exception is the change from ABE to TRS (both from 1947 to 1979 and from 1979 to 2019), which is generally related to the implementation and growth of tree cover in streets and squares, in residential areas and in previously industrial areas (following the demolition of factory buildings).

The area covered by TRS cover has remained relatively constant for the analyzed period. However, vegetation patches with this cover experienced a fair number of changes (Fig. 4; Table 2). In fact, only approximately half of the TRS cover was maintained in each of the transitions (from 1947 to 1979 and from 1979 to 2019), while the rest was transformed mainly to ABE, but also HER cover.

As also seen in Table 2 and Fig. 4, for both time intervals, areas of HER cover have also been gradually substituted, in considerable proportions, by areas of TRS cover (309.84 ha for 1947–1979, 282.13 ha for 1979–2019). The category of HER cover went from being the predominant class, in 1947 (40% cover), to one of the least abundant land cover categories (10% cover), being surpassed by both ABE and TRS.

The categories of Sparsely Vegetated – Terrestrial (SPV) and Sparsely Vegetated – Aquatic (AQU) are strongly associated with the coastal and river lines (beaches, cliffs, sea, and watercourses), that have remained relatively stable at the city level (Fig. 4; Table 2). However, it should be noted that a relatively large surface of SPV cover has been replaced by ABE, especially in the period 1979–2019. The changes seen in the category of SPV are related to tidal variation, construction in previously

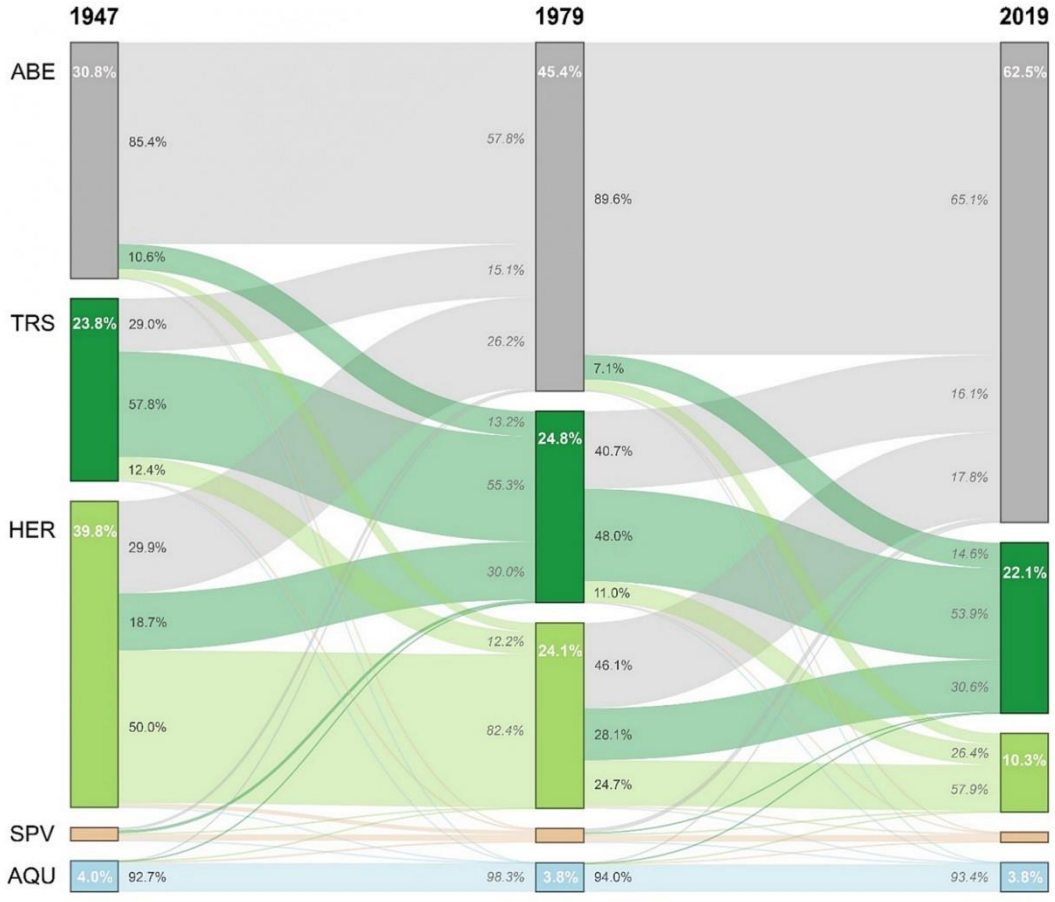



**Fig. 4.** Diagrammatic representation of the evolution of land cover in Porto, from 1947, to 1979 and to 2019 (created with "SankeyMATIC", at www.sankeymatic.com). Land cover categories: ABE, Artificial Built Elements; TRS, Trees and Shrubs; HER, Herbaceous; SPV, Sparsely Vegetated Terrestrial; AQU, Sparsely Vegetated Aquatic. White values refer to the proportions of each land cover category for each of the three years; dark values indicate: 1) the proportion of the original land cover that followed that path (regular text on the right side of the bars), 2) the proportion of the target land cover that followed that path (italicized text on the left side of the bars); only the values that relate to transformations that occurred in over 100 ha appear in the figure.

**Table 2**
Land cover conversion matrix from 1947 to 1979 and from 1979 to 2019 (area, ha).

| Land cover | | 1979 | | | | | Total (1947) | Change |
|---|---|---|---|---|---|---|---|---|
| | | ABE | TRS | HER | SPV | AQU | | |
| 1947 | ABE | 1092.96 | 135.89 | 48.07 | 2.53 | 0.41 | 1279.86 | + 47.7% |
| | TRS | 286.18 | 570.99 | 122.13 | 9.01 | 0.19 | 988.50 | + 4.5% |
| | HER | 494.60 | 309.88 | 827.07 | 22.36 | 0.33 | 1654.24 | − 39.3% |
| | SPV | 14.81 | 16.02 | 5.90 | 33.44 | 1.68 | 71.85 | + 7.8% |
| | AQU | 1.55 | 0.29 | 0.22 | 10.08 | 154.15 | 166.29 | − 5.7% |
| **Total (1979)** | | 1890.10 | 1033.07 | 1003.39 | 77.42 | 156.76 | 4160.74 | |

| Land cover | | 2019 | | | | | Total (1979) | Change |
|---|---|---|---|---|---|---|---|---|
| | | ABE | TRS | HER | SPV | AQU | | |
| 1979 | ABE | 1693.55 | 134.20 | 58.70 | 2.77 | 0.88 | 1890.10 | + 37.7% |
| | TRS | 420.03 | 496.09 | 113.27 | 3.19 | 0.49 | 1033.07 | − 10.9% |
| | HER | 462.84 | 281.71 | 247.79 | 6.39 | 4.66 | 1003.39 | − 57.3% |
| | SPV | 22.02 | 7.74 | 8.42 | 34.90 | 4.34 | 77.42 | − 32.3% |
| | AQU | 3.79 | 0.45 | 0.09 | 5.14 | 147.29 | 156.77 | + 0.6% |
| **Total (2019)** | | 2602.23 | 920.19 | 428.27 | 52.38 | 157.67 | 4160.74 | |

vacant lots, abandonment of sediment extraction sites and regeneration of previously deforested sites, whereas for AQU it mainly reflects tidal variation, the artificialization of coastal and riverfront and the built-up of bridges. For the remainder of this article, SPV and AQU evolution will not be discussed further, as it is outside the main scope of this research.

### 3.2. Changes in vegetation cover

Now focusing on vegetation patches, the results revealed substantially different patterns of land cover transformation for TRS and HER categories. Regarding arboreal vegetation (Fig. 5.a), over 40% of the study area was covered by TRS at some point between 1947 and 2019. While a considerable proportion of the territory faced the loss of TRS cover (14.3% of the study area), this was somehow compensated by the gain in TRS cover in other areas (12.7% of the study area).

A significant portion of the city (7.5%) has been permanently covered by TRS since 1947, mainly organized in large patches (Fig. 5.a). To a similar extent, some areas (6.7% of the study area) experienced a gain of TRS cover between 1947 and 1979 but were later occupied by artificial elements between 1979 and 2019.

In contrast with the more balanced changes in tree cover, the evolution of herbaceous vegetation identifies a clear dominant trend towards the loss of the majority of patches of HER cover (Fig. 5.b). While almost half of the city was covered with herbaceous vegetation at some point between 1947 and 2019, the loss of HER cover occurred in about a third of the study area (32.8%) for the same period. In about 10% of the territory, HER cover was replaced by TRS. However, the most common change was from HER to ABE (in over 20% of the study area). On the contrary, only 5.2% of the city area corresponds to persistent herbaceous patches, from 1947 to 2019. Some new herbaceous patches were created in the analyzed period, but the gain of HER cover is not expressive at the city scale.

Considering all vegetated areas (Fig. 5.c), whether covered by herbaceous or wooded vegetation, it becomes clear that some large areas have been spared from construction since, at least, 1947, and they are mainly concentrated in the western, eastern, and northern sections of the city (amounting to 25.3% of the study area). On the other hand, more than one third of the territory (35.1%) has experienced the complete loss of vegetation cover; this trend is very noticeable in the periphery of the city, due to the urban sprawl of the second half of the 20th century (Fig. 5.c). In this overall analysis, the areas that gained vegetation cover were almost negligible.

This analysis of land cover trajectories allowed to detect which areas have been continuously covered by vegetation, displaying a higher stability and higher probability of habitat continuity. As highlighted in Fig. 6, around 25% of the territory has been consistently covered by vegetation, but approximately half of this area experienced significant habitat changes, transitioning from wooded to herbaceous vegetation or vice-versa. Patches of relatively stable habitat are restricted to 12.7% of the city surface and include wooded and herbaceous habitats in similar proportions. Habitats with continuous tree and shrub cover are scattered throughout the entire study area, while the habitats with continuous herbaceous cover are concentrated in the western, eastern, and northern sections.

This research allowed for the identification of the main sections of the city that have a greater conservation value based on the criteria of habitat temporal continuity, while also considering their susceptibility to habitat loss, based on their protection status in urban planning programs, current land use, ownership, and accessibility (Fig. 7). This spatially explicit representation can be particularly useful for communication and knowledge dissemination. Indeed, while the areas with high probability of habitat continuity are evenly distributed throughout the city, the eastern and northern sections face a lack of protection of these important green spaces. The majority of the older vegetation patches in the northern and eastern section is located in private undeveloped land, unlike the most western section, where they are generally integrated in parks and gardens.

## 4. Discussion

The global trend of increasing urbanization and loss of vegetated areas (Güneralp et al., 2020; Radwan et al., 2021; Richards & Belcher, 2020) was also experienced in Porto. This phenomenon of declining vegetation cover being associated with urban expansion and densification has been reported by numerous authors in cities and metropolitan areas around the world (e.g. Lennert et al., 2020; Zaitunah et al., 2021; Zubair, 2021). Some authors have also investigated the relation between urban expansion and vegetated areas for the particular case of Porto. For example, Madureira et al. (2011) analyzed the evolution of the green structure in Porto and highlighted its severe decline and fragmentation throughout the 20th century, especially for agricultural areas. In a comparison between multiple cities, Bagan and Yamagata (2014) noticed a similar pattern for Porto, where the increase in urban area resulted in the destruction of forest, cropland and grassland.

Nevertheless, except for a few cases, the research on urban site history or urban land cover trajectories is still very incipient, especially at the local level. The local landscape level is defined by Opdam et al. (2013) as the "areas where physical landscapes interact directly with

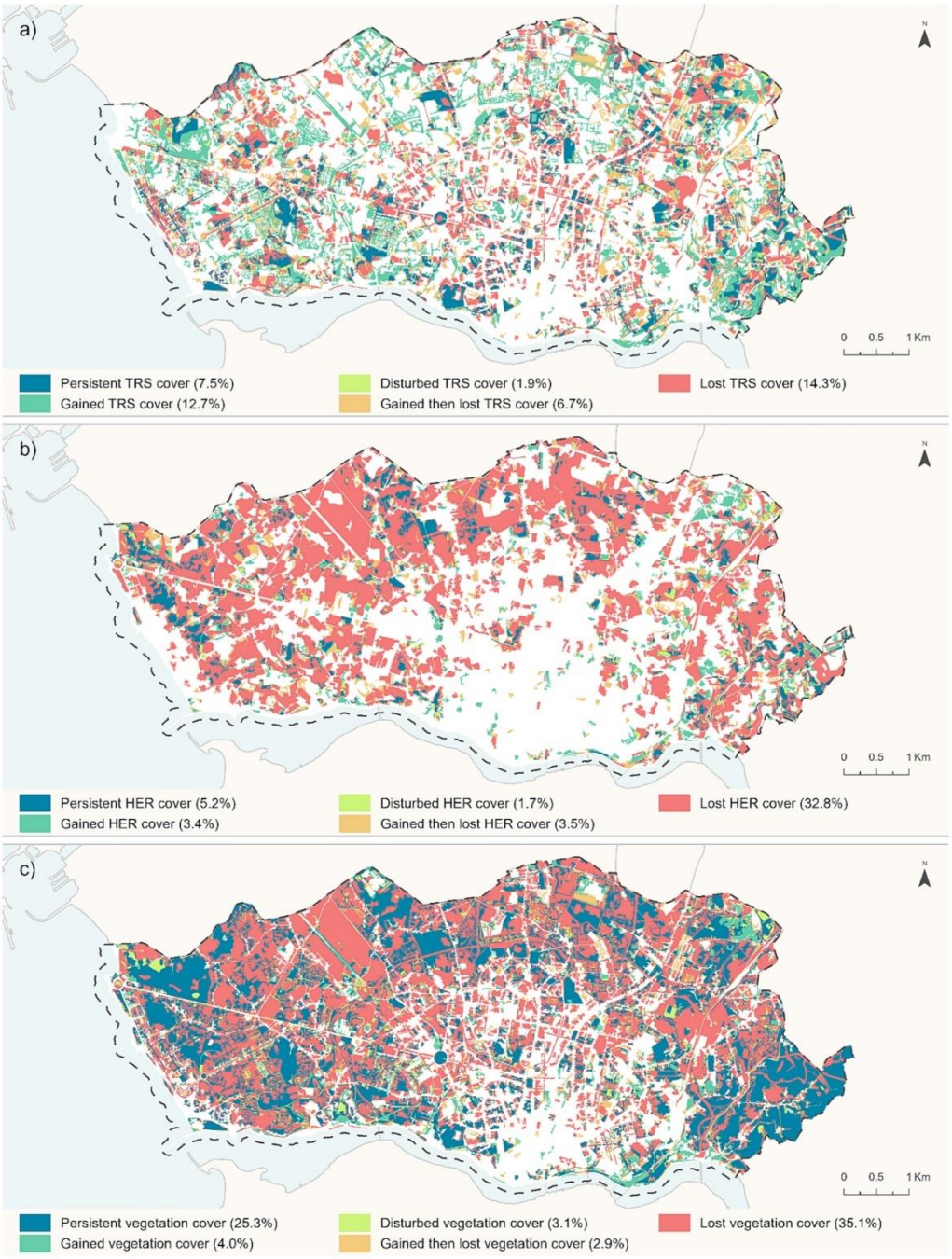



**Fig. 5.** Patterns of land cover change involving: a) TRS, Trees and Shrubs, b) HER, Herbaceous, and c) overall vegetation.

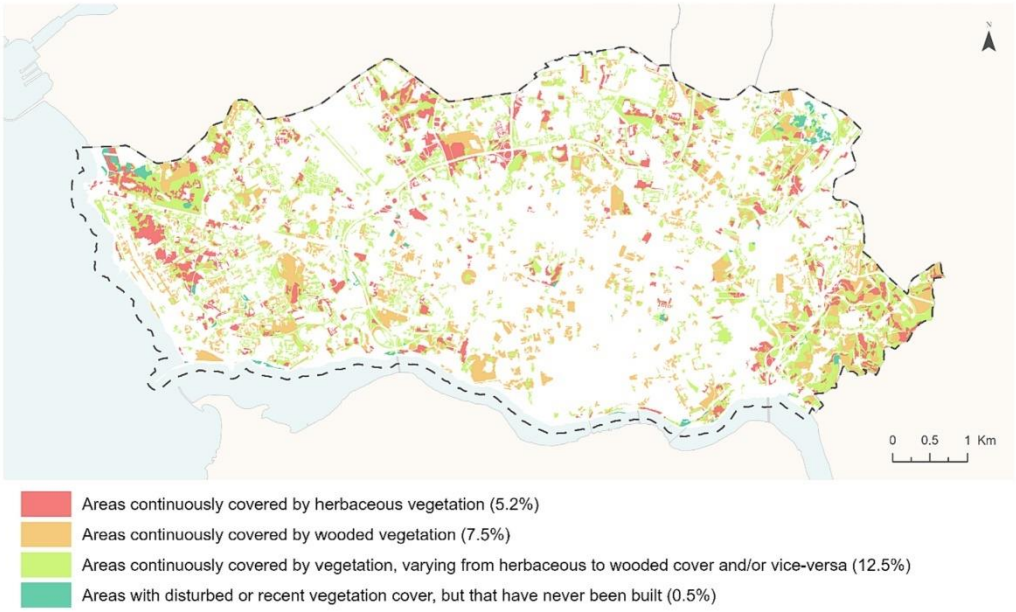



**Fig. 6.** Vegetated areas with higher stability and higher probability of habitat continuity.

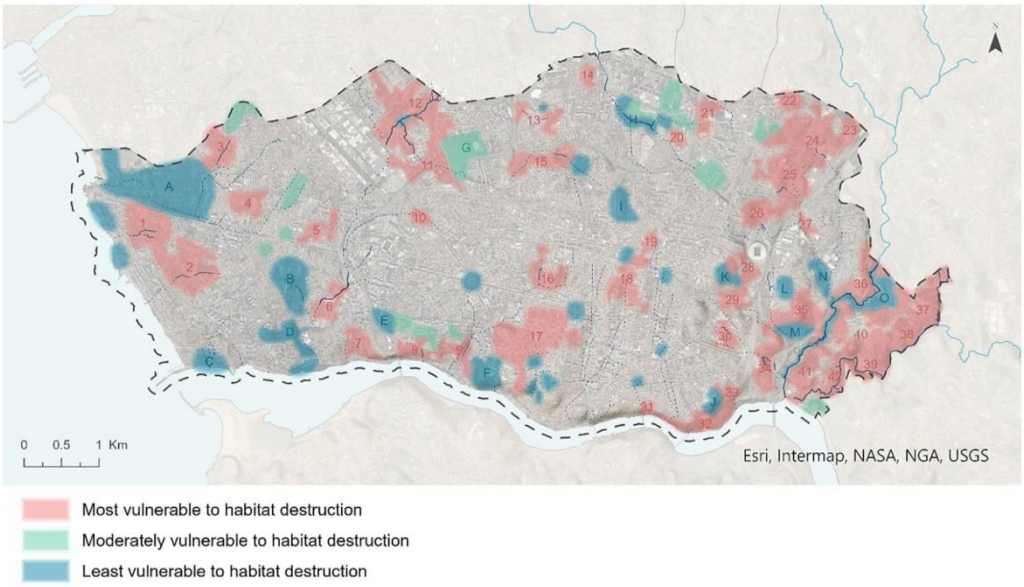



**Fig. 7.** Main sections of the city with higher habitat continuity, graded by their vulnerability to habitat destruction; for a complete legend see appendices (source of background imagery: Direção-Geral do Território, 2018).

social networks of land owners, managers, and landscape users". This is particularly relevant in urban landscapes, where the ecological dynamics are constantly affected by local scale decisions such as the planning, design and management of individual sites and infrastructures (Brown, 2017; Kremer et al., 2016). The study of land cover trajectories of Porto unraveled the history of each site and allowed to infer the temporal continuity of each vegetation patch, which was achieved at a very fine scale for the entire city. Past land use and land cover have an impact on ecosystem functioning, as they influence current landscape conditions and affect future responses to environmental change (Foster

et al., 2003; Ramalho & Hobbs, 2012). The current assemblies of urban biodiversity are a result of the interaction between landscape heterogeneity and connectivity, which are influenced by the age and history of each site or habitat patch (Alberti et al., 2020; Alberti & Wang, 2022; Cadenasso et al., 2006; Foster et al., 2003). Older habitats, i.e. those that are more stable and that underwent the least transformation, are considered to harbor higher biodiversity levels (Janssen et al., 2017; Nordén et al., 2014; Raduła et al., 2020). For this reason, habitat age or temporal continuity can be used as a valuation criteria for the conservation of urban habitats (Jarvis & Young, 2005; Wittig & Schreiber, 1983).

The analysis of land cover change in Porto showed a highly dynamic urban landscape. Only around 40% of the study area has remained relatively stable in terms of land cover during the study period; this value seems to be a bit lower than the average reported for other southern European cities (e.g. Frondoni et al., 2011) and it mostly regards land that was already urbanized in the mid-20th century. The most noticeable land cover transformation in Porto is related to urbanization processes that drastically reduced and fragmented vegetation patches, which is comparable to other urban areas (Tello et al., 2020; Zaitunah et al., 2021).

Tree and shrub (TRS) cover revealed a dynamic history in Porto since 1947, despite maintaining a constant proportion in the city throughout the years – a fair portion of the old TRS patches were destroyed (597 ha or 14.3% of the study area), but others were created elsewhere in a similar extent (529 ha or 12.7%). Large patches of forestry and wooded crops were gradually replaced by urbanization (ABE), especially in the periphery. It is also noteworthy the loss of TRS cover in smaller spaces, spread throughout the center and in the western extremity (the oldest parts of the city), which once formed a network of tree-covered private gardens and tree-lined streets which was lost over time. The areas that experienced a gain in TRS cover reflect two main trends, both of which occurred mainly in patches previously dominated by herbaceous vegetation: 1) the abandonment of former agricultural fields, where the natural course of ecological succession originated wooded habitat patches; 2) the construction of residential buildings surrounded by wooded green spaces. Around 314 ha (or 7.5% of the study area) consists of land continuously covered by trees and shrubs. Most of this area corresponds to older public parks and gardens (e.g., Crystal Palace Gardens and Passeio Alegre Garden; Fig. 7), or old farms that have been converted into public parks more recently (e.g., Covelo Park and S. Roque Park; Fig. 7), but some forestry still remains in the eastern and north-eastern parts of the city (particularly in the areas of Areosa and Areias; Fig. 7). The inherent nature of forested areas, with periodic clearings and the use of monospecific cultures, can have negative effects on biodiversity levels (Liu et al., 2018; Pohjanmies et al., 2021), so its conservation value is probably limited. In contrast, the wooded habitat patches located in parks and gardens present a higher stability and are expected to harbor a more diverse and abundant array of species (Nielsen et al., 2014; Vasquez & Wood, 2022). Unlike what happened with the herbaceous cover, a significant amount of new TRS habitats was created between 1947 and 2019. This tree and shrub cover that developed more recently in vacant lots or previously cultivated land, with a multi-layered vegetation structure (which is not commonly observed in public parks and gardens) due to the lack of management, can also develop interesting levels of biodiversity, but faces additional challenges associated with the presence of invasive species, little social value and low acceptance by local residents (Filibeck et al., 2016; Gaertner et al., 2017).

The areas occupied with herbaceous (HER) cover have suffered a drastic reduction since 1947, which was particularly severe between 1979 and 2019; in the overall picture, around one third of the territory (1367 ha) experienced the loss of herbaceous habitats. The development of new built structures and impervious surfaces in Porto took the place of previously open spaces, which are usually covered with herbaceous vegetation, in a similar scenario as other geographic contexts (e.g. Tello et al., 2020). The creation of new herbaceous patches was insignificant (only 3.4% of the study area, 141 ha) and corresponds to areas where previously forested land was cleared for future urban development and areas where old industrial or residential urban fabric was demolished and not yet replaced. Patches with persistent herbaceous vegetation occur in only 5.2% of the city (216 ha) and most of them express an agricultural past and were historically managed in the form of arable land or pastures. However, nowadays, most of these areas correspond to vacant lots without current defined use (where the herbaceous vegetation is kept by infrequent mowing or grazing), some have been absorbed by parks or gardens and converted to lawns, and only a small fraction retains an agricultural profile. The larger and older patches of herbaceous habitats are concentrated in the western extremity (the surrounding area of Nevogilde and Ervilheira streams), in the northern area (around Quinta da Prelada, Viso and Requesende), at the northeastern zone (around Contumil), and in the eastern portion of the city (particularly around the areas of Pinheiro de Campanhã, Tirares, Granja and Furamontes; Fig. 7). Unlike most of the older wooded habitats, which are integrated in large parks and gardens, most of these old herbaceous patches are located in vacant lots and small cultivated areas, thus being quite vulnerable to being displaced by new urban developments.

In order to maintain sufficient levels of ecosystem functioning, to promote urban biodiversity and ultimately to benefit the health and well-being of the residents of Porto (Aerts et al., 2018; Zari, 2018), vegetation patches and habitats should be preserved as they are becoming increasingly scarcer. Generally speaking, the biodiversity of different habitat types is enhanced when these habitats are older (Nordén et al., 2014), which can be due to a more complex vegetation structure and a more diverse collection of microhabitats that can harbor a higher diversity of species, as well as also factoring the time that certain species can take to colonize new habitat patches after dispersion (Janssen et al., 2017). The influence of habitat persistence varies according to several species life traits, especially their habitat specificity, longevity, and dispersal capability (Lira et al., 2019). Specialist, long-lived, and/or dispersal-limited species tend to show a more delayed response to habitat change (e.g. Krauss et al., 2010; Löfvenhaft et al., 2004; Sang et al., 2010). A similar pattern was discovered in a previous study focused on the patches conserving natural vegetation within the whole metropolitan area of Porto, where even small areas kept a substantial diversity of amphibian and reptile species with limited dispersal capabilities (Ribeiro et al., 2009). The maturity of vegetation, particularly trees, besides influencing the occurrence of microhabitat niches (Janssen et al., 2017), has also implications on the provision of several other ecosystem services beneficial for humans (Jonsson et al., 2020).

While the relationship between the age or continuity of urban habitats and their biodiversity levels is fairly understudied, several authors have investigated this association in other wooded and herbaceous habitats. It has been shown that forests and woodlands with a higher continuity in time exhibit a higher species richness, especially due to the occurrence of specialist species; these are associated with particular habitat niches that take time to develop as the forest stand matures, such as rough bark, tree cavities or deadwood (Janssen et al., 2017; Nordén et al., 2014; Siitonen & Saaristo, 2000). The city of Porto has, so far, succeeded at preserving a substantial portion of its older wooded habitats, by including them in public parks and gardens that provide multiple benefits for the citizens. A higher level of biodiversity in urban parks is positively associated with direct gains in the health and well-being of their users (Cameron et al., 2020; Schebella et al., 2019; Wood et al., 2018). Thus, in order to maximize the benefits of these old tree-covered habitats, it is necessary that their management considers the promotion of biodiversity and other ecosystem services. For example, it is important to allow trees to reach maturity, encourage the occurrence of multiple layers of vegetation and support the creation of diverse microhabitats, often contradicting traditional maintenance practices (Han et al., 2022; Le Roux et al., 2014; Nielsen et al., 2014; Threlfall et al., 2017).

Historical parks with restricted access, but belonging to institutions of public interest, have also an important role in the preservation of old woodlands in Porto, and they generally present lower disturbance levels due to reduced intensity of use. Here, this type of green space has its main origins in old recreational farms and manor house gardens and they can present a high biodiversity potential (Lõhmus & Liira, 2013). These areas are not publicly accessible, but are generally owned by institutions of public interest, such as universities, schools, health facilities, local government, etc. While these are likely to be maintained in the long run, their green spaces are not considered in spatial planning and are thus more susceptible to habitat destruction than public green spaces, and, consequently, its future preservation and adequate management should also be promoted. Likewise, some residential gardens are also relevant for the maintenance of older wooded habitats, especially near the city center where the urban matrix is also from an earlier period. These areas also have biodiversity conservation interest, especially when considered collectively (Doody et al., 2010; Goddard et al., 2010; Thompson et al., 2003). These are particularly susceptible to urban development and, therefore, quite challenging to preserve. We suggest the engagement of the population towards biodiversity conservation practices and the implementation of restrictions to further land development in these areas, accompanied by benefits for the involved homeowners (Goddard et al., 2010; Parris et al., 2018).

Similarly to wooded habitats, there is also a relation between herbaceous habitat age or continuity and its species richness (Inoue et al., 2021; Radula et al., 2020), although it is still an understudied topic. In fact, herbaceous habitats, particularly grasslands, have been neglected by ecologists, land managers and planners, possibly due to the misconception that these are associated with land degradation after deforestation and other disturbances (Veldman et al., 2015). Urban grasslands are particularly affected and are often left out of conservation plans (Hüse et al., 2016). We have revealed a similar pattern in the city of Porto – while most of the relevant woodland patches have been safeguarded in parks and gardens, most of the old herbaceous patches have been lost due to urbanization or lack of maintenance. As an exception, a few herbaceous patches have also been integrated in public parks (namely City Park and Oriental Park; Fig. 7) and are likely to be maintained in the long run. However, these have been converted into lawns with dubious ecological value. The high frequency of mowing in these habitats is related to lower levels of plant, microorganism and invertebrate species richness (Chollet et al., 2018; Helden et al., 2018; Norton et al., 2019). The diversification of urban herbaceous habitats, so as to include different plant compositions, different heights and different uses, has the potential to generate considerable benefits for biodiversity. When adequately managed, urban herbaceous habitats, in the form of meadows, semi-natural grasslands, arable fields, etc., can provide valuable ecosystem services and harbor high biodiversity levels (Klaus, 2013; Onandia et al., 2019). Considering their extreme scarcity and lack of protection in the city of Porto, we believe that older herbaceous habitats should be considered as top priority regarding urban biodiversity conservation. To improve the biodiversity interest of herbaceous habitats in Porto, we suggest the promotion of a diverse vegetation community, aided by replanting native species and controlling invasive species, and the reinforcement of habitat connectivity amongst patches. The prospective loss of these vegetation patches at the city scale would contribute not only to the general trends of habitat destruction, but also to the trends of species extinctions that have already been described at an international level. For example, the European Environment Agency (2021) has recently reported the decline of farmland birds and grassland butterflies in EU member states, with both fauna groups being strongly associated with herbaceous habitats.

The most effective and cost-efficient strategy for urban habitat conservation involves the preservation of older habitat patches, but regeneration or restoration can be an alternative or complementary solution (McKinney, 2002). When considering this solution, attention must be given to the history of former land uses of each targeted vegetation patch, as well as its landscape context, as they can influence the biodiversity outcomes and other ecosystem services (Foster et al., 2003; Vandewalle et al., 2014). Habitat restoration should also take advantage of spatial–temporal connectivity of the patch (Uroy et al., 2021; Zhao et al., 2021), i.e. the restored habitat should emerge at, or near, a place where that habitat type has occurred previously, to maximize the flow of biological resources to the new habitat patch. This is particularly important in the case of low habitat availability at a larger scale and for species with low dispersal capability (Huang et al., 2020; Martensen et al., 2017). This way, older habitats, which can act as refuge for some species, can serve as a source for recolonization of the newly created favorable habitats.

The municipality of Porto has showed a growing interest in environmental issues in recent years, with plans to expand and connect its green infrastructure and with some interventions based primarily on the adaptation to climate change and, on a lesser degree, on the conflict between native and exotic species (Câmara Municipal do Porto, 2020, 2021a, 2023). However, the long-term plan for biodiversity conservation is still to be concretized, as most goals, actions and timeframes are not explicit yet. Although there are prospects for creating new public green spaces, the prioritization criteria are not discernible. This research could serve as a starting point for the definition of a future habitat and biodiversity conservation plan or program, as it provides crucial information for habitat restoration or expansion in Porto and recommendations for the design and management of green areas. Figs. 5-7 can help to identify priority areas for these types of interventions on wooded or herbaceous habitats, which should preferably occur near older vegetation patches, sites that have never been built and/or places where vegetation cover was recently lost.

The use of land cover trajectories seems to be an appropriate method to infer the degree of urban habitat continuity, with the main advantage of being a relatively simple and fast procedure, if adequate data is available, and that does not require expert knowledge. This method produces spatially explicit information, and its format has a high aptitude for the transfer of knowledge between the multiple actors in the design, planning and management of urban environments, from ecologists to landscape architects, urban planners, decision makers, and other stakeholders. For this exercise, we examined the evolution of land cover in Porto using three different time points, for a total period of 72 years. Although it was not possible due to limited resources and lack of available data, for improved results we suggest expanding the timeframe into the past and using shorter time intervals, to better capture the rich history and the fast-paced dynamics of this urban area. This method of spatial prioritization for the conservation of urban habitats can be enriched with information about habitat structure, composition, species richness and abundance of multiple taxa. Other authors have also used habitat connectivity (Lv et al., 2019; Mollashahi et al., 2020; Zhao et al., 2021), climate beneficiation (Norton et al., 2015), social values (Whitehead et al., 2014) and biodiversity quality (Jalkanen et al., 2020) to define priority habitats in cities.

There are a multitude of factors influencing the outcome of land cover evolution in a city, but urban planning, design and management have a central role in paving the way for more biodiverse and sustainable cities (Hersperger et al., 2018; Huang et al., 2018). City planners, designers and managers need to acknowledge that urban areas have the potential to harbor high levels of biodiversity and need to start integrating biodiversity concerns in their plans, policies and programs (Parris et al., 2018; Zari, 2018). Planning, design and management decisions that affect the pattern and composition of the urban landscape can also impact urban biodiversity, and, hence, the quality of life of human urbanites (Zari, 2018); it should be based on frequently updated and comprehensive information, displayed in a spatial framework, which must also include ecological data (Jarvis & Young, 2005). Similarly, ecologists need to address the needs of urban planners and managers regarding biodiversity conservation, translate them into ecologically relevant questions, and provide appropriate feedback that is

useful at the scale of intervention (McDonnell & Hahs, 2013). Ultimately, the transformation of the urban landscape should be supported by multidisciplinary teams, but always including landscape and/or urban ecologists (Jarvis & Young, 2005; McDonnell & Hahs, 2013; Parris et al., 2018), so that science and research translates into real life practices and interventions, moving towards the greener, biodiverse and sustainable cities of the future.

## 5. Conclusion

Due to their nature, urban areas face a lack of vegetation, green spaces and habitats to support their biodiversity and ultimately the health and well-being of their citizens. In this study, we were able to identify the main urban habitat patches in the city of Porto, as well as their land cover history since the mid-20th century. Although around a third of the surface of the city is currently covered by vegetation, most of the vegetated patches have experienced significant disturbance and frequent transformations between herbaceous and wooded habitats. Persistently wooded areas are rather scarce, but most are already protected in large parks and gardens. Areas continuously covered by herbaceous vegetation are even rarer in Porto and they are constantly disregarded by politicians, urban planners and even conservationists, being left out of urban planning and conservation programs.

Spatially explicit historical land cover data, such as the information presented here, can be easily integrated in spatial planning projects. It should, however, be complemented with more detailed information about habitat structure and species composition. We should aim to preserve, restore and, ideally, expand older habitats, whether occupied by trees, shrubs, or herbaceous vegetation. Older habitats allow for the formation of diverse microhabitats and the accommodation of diverse species over time, contributing for a richer biodiversity at the city or regional level. Regarding the dynamics of urban ecosystems, the conservation of herbaceous habitats seems to be particularly challenging. However, if managed properly, these habitats can provide fundamental ecosystem services and harbor important species that are becoming increasingly rare.

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## CRediT authorship contribution statement

**Filipa Guilherme:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **José Alberto Gonçalves:** Resources, Writing – review & editing. **Miguel A. Carretero:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition. **Paulo Farinha Marques:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

## 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.

## Data availability

Data will be made available on request.

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**Appendix A List of the mains priority areas for the conservation of habitats with higher continuity (complementing Fig. 7)**

| Areas comprising mainly parks and gardens | Areas comprising mainly undeveloped land and/or private property | | |
|---|---|---|---|
| A – City Park | 1 – Ribeira de Nevogilde | 15 – Regado | 29 – 25 de Abril |
| B – Serralves Park | 2 – Ribeira da Ervilheira | 16 – Burgães / Lapa | 30 – Godim |
| C – Passeio Alegre Garden | 3 – Ribeira de Aldoar | 17 – Cedofeita | 31 – Fontainhas |
| D – Pasteleira Park | 4 – Mata de Aldoar | 18 – Santa Catarina | 32 – Quinta da China |
| E – Botanical Garden | 5 – Pinheiro Manso | 19 – Lima | 33 – Formiga |
| F – Crystal Palace Garden | 6 – Lordelo | 20 – Lamas | 34 – Pinheiro de Campanhã |
| G – Prelada Park | 7 – Ribeira do Ouro | 21 – Areosa Ocidental | 35 – Corujeira / Monte da Bela |
| H – Asprela Park | 8 – Via Panorâmica | 22 – Areosa Oriental | 36 – Tirares / Pego Negro |
| I – Covelo Park | 9 – Ribeira de Vilar / Pena | 23 – Ranha | 37 – Areias |
| J – Nova Sintra Park | 10 – Francos | 24 – Currais | 38 – Furamontes |
| K – São Roque Park | 11 – Prelada | 25 – Contumil | 39 – Granja |
| L – Corujeira Park | 12 – Viso / Requesende | 26 – Salgueiros | 40 – Azevedo |
| M – Quinta da Bonjóia | 13 – Telheira | 27 – São Roque da Lameira | 41 – Quinta da Revolta |
| N – future Alameda de Cartes Park | 14 – Azenha | 28 – Lameira de Cima | 42 – Rio Torto |
| O – Oriental Park | | | |

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**Article III**

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# Mapping multigroup responses to land cover legacy for urban biodiversity conservation

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ABSTRACT

Urban biodiversity plays a crucial role in the functioning of urban ecosystems and significantly impacts the well-being and quality of life for city residents. By focusing on the city of Porto as a case study, the influence of local-scale land cover evolution on urban biodiversity is investigated, using species richness of birds, reptiles, and amphibians as indicators, within a multimodel inference framework. The results underscore the importance of past land cover and land cover legacy in shaping urban biodiversity. Birds, reptiles, and amphibians respond positively to older vegetation patches but negatively to long-established urban areas. Birds exhibit adaptability by positively responding to recent vegetation, while amphibians tend to avoid newly vegetated zones. The fragmented distribution of amphibians and reptiles in Porto suggests limited mobility and a potential delayed response to habitat loss and isolation. Reptiles benefit from both wooded and herbaceous habitats, emphasizing the importance of local spatial diversity, while water elements are critical for amphibians, although many aquatic habitats in the urban context may not be suitable. Modeling results guide the identification of priority areas for urban biodiversity conservation in Porto, informing decision-makers, urban planners, and conservationists. This spatially explicit research aids efforts to create more ecologically resilient and biodiverse urban environments. It highlights the role of historical land cover and the unique responses of different vertebrate groups to urbanization, contributing to our understanding of urban biodiversity dynamics and sustainable urban development.

## 1. Introduction

Urban biodiversity is fundamental for urban ecosystem functioning (Harrison et al., 2014; Millennium Ecosystem Assessment, 2005; Zari, 2018) and ultimately for the health, well-being, and quality of life of urban residents (Marselle et al., 2021). Cities are often located in biologically-rich areas (Ives et al., 2016; Kowarik, 2011) and urbanization has detrimental effects on species and habitats (Fraissinet et al., 2023; Liang et al., 2023; McKinney, 2002; Simkin et al., 2022; Tilman et al., 2017). However, urban areas can contribute to biodiversity conservation, as they often integrate a diverse mosaic of semi-natural and man-made habitats, home to unique assemblies of flora and fauna species, even including rare or threatened species (Jokimäki et al., 2018; Müller et al., 2013; Spotswood et al., 2021). Urbanization is a complex and dynamic process, driven by a multitude of interacting social, economic, and environmental factors (Shaw et al., 2020). Land cover change is one of its main consequences, often resulting in the loss and fragmentation of vegetation, natural or semi-natural habitats, and agricultural land (Güneralp et al., 2020; Richards and Belcher, 2020), with deleterious effects on local species communities (Callaghan et al., 2021; Concepción et al., 2015; Ross and Henkanaththegedara, 2019).

Urban species assemblies are the result of the interaction between

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landscape heterogeneity and connectivity, which depend on the age and history of each site or habitat patch (Alberti et al., 2020; Alberti and Wang, 2022; Cadenasso et al., 2006; Foster et al., 2003). While this topic remains relatively understudied in urban contexts, several authors have investigated the relationship between persistence or age of different types of habitats and their biodiversity levels, in other ecosystems. In general, older habitats, i.e. those that are persistent in time and have experienced less changes, exhibit higher levels of biodiversity (Janssen et al., 2017; Nordén et al., 2014; Radula et al., 2020). Habitat persistence can influence the occurrence of diverse organismal groups over time, by interfering with different ecological processes. For instance, by generating time-lagged responses, it affects metapopulation and metacommunity dynamics, such as dispersal, (re)colonization, and extinction; this can lead to phenomena of extinction debt or immigration (or species) credit (Lira et al., 2019; Swan et al., 2021; Uroy et al., 2021). Additionally, persistent or older habitats usually present a more complex vegetation structure and a more diverse collection of habitat niches that take time to develop in the ecological succession, such as tree cavities or wood decay, creating favorable conditions for a higher diversity of organisms, particularly specialist species (Janssen et al., 2017; Nordén et al., 2014). Species life-history traits determine their different responses to land cover change and persistence, namely their habitat specificity of different life stages, longevity, and dispersal capability (Lindenmayer et al., 2023; Lira et al., 2019). Species that are habitat specialists at any life stage, long-lived, and with restricted dispersal, tend to show a more delayed response (e.g. Krauss et al., 2010; Löfvenhaft et al., 2004; Sang et al., 2010) and are, thus, more susceptible to environmental change. For these reasons, habitat age or persistence can be considered as a good indicator of urban biodiversity value and be can used to inform urban habitat conservation programs, as well as to support evidence-based decision-making regarding urban landscape planning, design and management (Jarvis and Young, 2005; Wittig and Schreiber, 1983).

The complexity and heterogeneity of the urban territory translate into additional challenges for spatial planning and management (Borgström et al., 2006), taking into consideration the intricate fabric of greener areas amidst a more artificial matrix. The ecological dynamics of the urban landscape is largely affected by local-scale decisions and interventions, related to the planning and design of individual sites, infrastructures, and community masterplans (Brown, 2017). Beyond the cooperation between multiple disciplines and stakeholders, data collection and spatial analysis must contribute to the integration of ecological information in urban planning, design, and management, i.e., generate "actionable knowledge" (Garrard et al., 2018; Zhou et al., 2019). The scale of analysis is particularly important when considering urban biodiversity preservation – the local scale is more closely related to the planning and management decisions that directly translate into site interventions that modify urban habitats (Ancillotto et al., 2019; Brown, 2017; Łopucki and Kiersztyn, 2015; Molné et al., 2023; Opdam et al., 2013).

In urban areas there is a generalized lack of data on species occurrence and abundance, which is even more severe at the local scale (Grafius et al., 2019) and for certain taxa, such as amphibians, reptiles, bats and particular groups of invertebrates (Faeth et al., 2011; Rega-Brodsky et al., 2022). When it comes to urban vertebrates, birds are the main choice for most researchers – they are good indicators of urban ecosystem condition, providing cheap and easy measurements, and are sensitive to changes in habitat structure and composition (Farinha-Marques et al., 2011). In contrast, urban herpetofauna (amphibians and reptiles) is poorly studied and needs a thorough analysis (Faeth et al., 2011; Rega-Brodsky et al., 2022) with most species being highly susceptible to local habitat transformation and fragmentation (Cordier et al., 2021; Delaney et al., 2021), phenomena that are especially noticeable in urban areas (Niemelä, 2011).

The scientific evidence coming from landscape ecology lays the groundworks for understanding the relationship between biodiversity and the spatially explicit environment in which it occurs in a given timeframe. Ecological modeling is a fundamental tool to predict the spatial variation in biodiversity, which is particularly useful in a context of high spatial complexity and heterogeneity, such as urban areas (Grafius et al., 2019). Spatial predictions can also be useful to tackle lack of biodiversity data in some locations. In urban biodiversity research, modeling analysis is often used to study the occurrence of particular species (e.g. Plummer et al., 2020) or patterns of species richness (e.g. Petersen et al., 2020).

In this article, we aim to investigate how the evolution of land cover, at a local scale, influences urban biodiversity. Using vertebrate species richness as an indicator of biodiversity levels, we test the influence of: 1) water elements, 2) current land cover, 3) past land cover, 4) age of vegetation cover, and 5) trend of vegetation cover change, on biodiversity, using a multimodel inference framework. Based on the results of species richness modeling, with the intent of producing "actionable knowledge", we aim to identify priority areas for the conservation of urban biodiversity for the case of Porto, Portugal. Based on the above-mentioned literature and on the knowledge of the system, we hypothesize that all studied animal groups (birds, reptiles and amphibians) are influenced by the current land cover and also reveal a response to land cover legacy (e.g., higher richness with more temporal stability), possibly in different forms due to life-history. Moreover, we predict that herpetofauna will display a stronger response to land cover change than birds, being more associated with older habitats, due to their limited dispersal capabilities; amphibians are also expected to present a stronger relationship with the presence of water, due to their life cycle requirements. If our expectations are met, urban planning and management needs to prioritize the preservation and expansion of the older habitat areas.

## 2. Methods

### 2.1. Study area

This research was conducted in Porto, a city located at the intersection of the Douro River with the Atlantic Ocean, in Northern Portugal (Fig. 1). Porto is a densely urbanized, medium-sized city (with around 42 $km^2$ and almost 232,000 inhabitants; INE, 2022) and it is at the core of a dynamic metropolitan area, comprised of 17 municipalities and around 1.7 million residents (AMP, 2022). The city benefits from a mild temperate climate (*Csb* regime, Koppen-Geiger classification; Peel et al., 2007); the latest climate records indicate a mean annual temperature of 15.3 °C and annual precipitation of 1174.0 mm (data for 2021; PORDATA, 2022).

Porto has experienced a dynamic land cover evolution in the recent past. While most of the territory was occupied by vegetation in 1947 (63.6 % cover), it has suffered a drastic increase in urbanized areas that completely dominate the territory in 2019 (62.5 % cover; (Guilherme et al., 2022). For the purpose of fauna survey and species distribution modeling, the study area was divided with a 200 × 200 m grid, originating 994 squares (those that included <50 % of municipal land were excluded).

### 2.2. Response variables

For the assessment of urban fauna species, 43 of the 200 × 200 m squares were selected to survey three representative groups of vertebrates: birds, reptiles, and amphibians (Fig. 1). The selection of the squares was made in order to capture the main trends of land cover evolution occurring in Porto since the mid-20th century (Guilherme et al., 2024).

The presence of birds, reptiles, and amphibians was recorded during the spring and summer (April to July) of 2019 and 2021. Birds were surveyed using visual and acoustic detection and identification, with point-counts of eight minutes, between 6.30 and 9.00 a.m., as near as

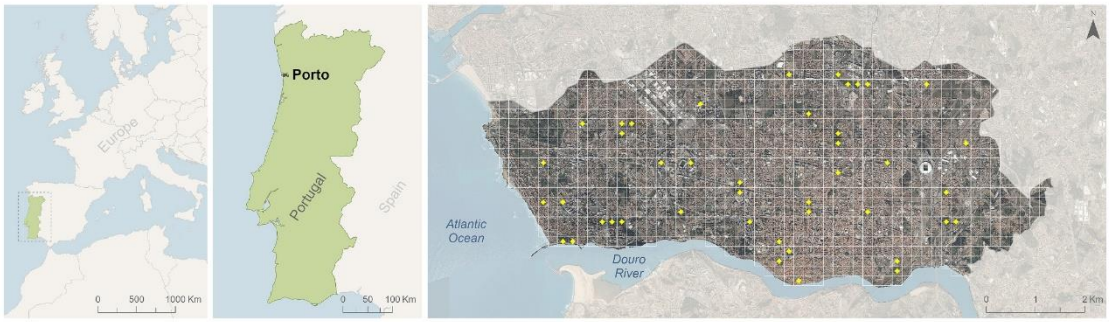



**Fig. 1.** Location of the study area (Porto, Portugal), and the selected squares for fauna sampling (yellow marks). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

possible to the center of the selected square (Rabaça, 1995; Sutherland et al., 2004). Only individuals which were explicitly using the site were recorded, i.e., birds that only flew over were not associated with the surveyed square (Huff et al., 2000). Reptiles and amphibians were surveyed through directed visual transects and refugia searching in the entire square; additionally, if water elements were present, netting was also used as a method to detect the larval stages of amphibians (Heyer et al., 1994; McDiarmid et al., 2014; Sewell et al., 2013). After evaluating the species accumulation curves for each site, bird surveys were performed six times in each square, while reptiles and amphibians were searched during four visits. This sampling intensity ensured saturation of species richness curves in this area (Farinha-Marques et al., 2023; Ribeiro, 2011). Finally, species richness was estimated for each of the fauna groups in the selected squares. This information was used to assess how land cover evolution affects species richness through a modeling framework.

### 2.3. Predictor variables

For the purpose of this study, predictors concern multiple sets of variables related to different land cover categories of the city of Porto and their evolution between three different time periods: 1947, 1979, and 2019, based on the work of (Guilherme et al., 2024). The mentioned research relied on the mapping of land cover in vectorial format in a GIS environment, following visual interpretation of remote sensing data (historic aerial photograph and satellite imagery), considering a minimum area of 2000 $m^2$ and a minimum width of 5 m. For the three dates (1947, 1979, and 2019), the study area was mainly distinguished in two broad categories: vegetated and non-vegetated areas. Vegetated areas were further segregated into tree and shrub cover (TRS) and herbaceous cover (HER). Non-vegetated areas were covered by artificial built elements (ABE), aquatic surfaces (AQU), or bare soil, sand, rock, or other sediment (SPV); only ABE was considered in the present work, as AQU and SPV play a reduced role in the land cover evolution in Porto.

The classification and mapping of the land cover of Porto for these three dates allowed for the assessment of the main changes in vegetation patches in terms of persistence, gain or loss, as well as the inference of the approximate age of each vegetation patch in three intervals: 0 to 39 years, 40 to 71 years, and 72 years or more.

Due to their importance for amphibians, and although they were not included as a measure of cover, the presence of water elements was considered as a predictor variable in a binary form, as most small-scale water features in this dense urban context were not adequately captured with the standard land cover mapping procedures.

To assess how different spatial scales can influence the distribution of different animal groups, all predictor variables were calculated considering two versions: 1) for each 200 × 200 m square, and 2) for a buffer of 200 m around each square (approximately a 600 × 600 m square). The 200 × 200 m square (hereafter named fine scale) is strongly related to the site scale and is associated with the home range and dispersal distances of the less mobile species of amphibians (Trochet et al., 2014), while the 600 × 600 m square (coarse scale) corresponds to the neighborhood scale and includes the dispersal range of common reptile species (Grimm et al., 2014). All bird species in the study area are expected to easily surpass these distances.

Groups of predictor variables, in both scales, were used to inform different models; the complete list of models and descriptions of predictor variables is explained in Table 1. Predictors with Spearman correlation coefficient $\geq 0.7$ were excluded from the same model to avoid multicollinearity issues (Daoud, 2017; Guisan and Zimmermann, 2000; Shrestha, 2020).

### 2.4. Modeling framework

To evaluate the effect of several land cover predictors on the species richness of birds, reptiles, and amphibians, the data analysis was organized according to five hypotheses: 1) presence of water; 2) current land cover; 3) past land cover; 4) age of vegetation cover; 5) trend of vegetation cover. Each of these hypotheses originated several groups of predictor variables, totaling 32 models (Table 1). We fit this set of competing models within a multimodel inference (MMI) framework to assess how well each model was supported by the data, instead of using a single best model (Burnham and Anderson, 2002). This allowed a direct comparison and a better assessment of the relative contribution of the influence of several land cover factors on the species richness of the different groups of animals under study. A null model (intercept model), assuming that all locations have the same probability of having the same species richness, i.e., that the land cover evolution does not affect species richness, was included as a sixth hypothesis (Table 1) in all analyses. This allowed testing whether the competing models for the previous hypotheses are more reliable than an intercept model (Burnham and Anderson, 2002).

We used the corrected Akaike information criterion (AIC; Akaike, 1973) for small sample sizes ($AIC_c$), as recommended when the ratio between $n$ (the number of observations used to fit the model) and $K$ (the number of parameters in the largest model) is <40 (Burnham and Anderson, 2002; Shono, 2000). We also limited the maximum number of predictors per model to four because of small sample sizes. For comparing among models, we calculated the $AIC_c$ difference, where $\Delta_i = AIC_c\ i - AIC_c\ min$ (Burnham and Anderson, 2002). Values of $\Delta_i \leq 2$ indicate models with good performance, while models with $\Delta_i < 7$ can be considered acceptable, although less supported by the data (Burnham and Anderson, 2002). These differences ($\Delta_i$) were used to derive Akaike weights ($w_i$), which represent the probability that a candidate model will be the best approximating and most parsimonious model given the data and set of models. Akaike weights are scaled between zero and one and

**Table 1**
List of hypotheses, competing models and predictors used in the multimodel inference framework.

| Hypothesis | Competing models | Predictors |
|---|---|---|
| *Water elements* (Chamberlain et al., 2007; Mbiba et al., 2021) | M1, M2: Water | Water (presence of water elements in 2019) |
| *Current land cover* (Amaya-Espinel et al., 2019; Aronson et al., 2014) | M3, M4: Type of vegetation cover in 2019 | TRS2019 (% tree and shrub cover in 2019)<br>HER2019 (% herbaceous cover in 2019) |
| | M5, M6: Vegetation cover in 2019 | Veg2019 (% vegetation cover in 2019) |
| | M7, M8: Artificial cover in 2019 | ABE2019 (% artificial cover in 2019) |
| *Past land cover* (Foster et al., 2003; Tello et al., 2020) | M9, M10: Type of vegetation cover in 1979 | TRS1979 (% tree and shrub cover in 1979)<br>HER1979 (% herbaceous cover in 1979) |
| | M11, M12: Vegetation cover in 1979 | Veg1979 (% vegetation cover in 1979) |
| | M13, M14: Artificial cover in 1979 | ABE1979 (% artificial cover in 1979) |
| | M15, M16: Type of vegetation cover in 1947 | TRS1947 (% tree and shrub cover in 1947)<br>HER1947 (% herbaceous cover in 1947) |
| | M17, M18: Vegetation cover in 1947 | Veg1947 (% vegetation cover in 1947) |
| | M19, M20: Artificial cover in 1947 | ABE1947 (% artificial cover in 1947) |
| *Age of vegetation cover* (Barth et al., 2015; Fernández-Juricic, 2000; McAlpine et al., 2015) | M21, M22: Age of tree and shrub cover | TRS72y (% tree and shrub cover existing for 72 years or more)<br>TRS4071y (% tree and shrub cover existing for 40 to 71 years)<br>TRS039 (% tree and shrub cover existing for <39 years) |
| | M23, M24: Age of herbaceous cover | HER72y (% herbaceous cover existing for 72 years or more)<br>HER4071y (% herbaceous cover existing for 40 to 71 years)<br>HER039y (% herbaceous cover existing for <39 years) |
| | M25, M26: Age of vegetation cover | Veg72y (% vegetation cover existing for 72 years or more)<br>Veg4071y (% vegetation cover existing for 40 to 71 years)<br>Veg039y (% vegetation cover existing for <39 years) |
| *Trend of vegetation cover change* (Fraissinet et al., 2023; Knick and Rotenberry, 2000) | M27, M28: Tree and shrub cover change | TRS72y (% tree and shrub cover existing for 72 years or more)<br>TRSLoss (% tree and shrub cover lost between 1947 and 2019)<br>TRSGain (% tree and shrub cover gained between 1947 and 2019, where it did not occur before)<br>TRSDisturb (% tree and shrub cover gained between 1979 and 2019, in a location where it occurred in 1947) |
| | M29, M30: Herbaceous cover change | HER72y (% herbaceous cover existing for 72 years or more)<br>HERLoss (% herbaceous cover lost between 1947 and 2019)<br>HERGain (% herbaceous cover gained between 1947 and 2019, where it did not occur before)<br>HERDisturb (% herbaceous cover gained between 1979 and 2019, in a location where it occurred in 1947) |
| | M31, M32: Vegetation cover change | Veg72y (% vegetation cover existing for 72 years or more)<br>VegLoss (% vegetation cover lost between 1947 and 2019)<br>VegGain (% vegetation cover gained between 1947 and 2019, where it did not occur before)<br>VegDisturb (% vegetation cover gained between 1979 and 2019, in a location where it occurred in 1947) |
| *Null model* (Burnham and Anderson, 2002) | M33: Null model | |

represent the proportional support for a particular model given all models. Additionally, we calculated the adjusted $R^2$ to estimate the models' explanatory power (Guisan and Zimmermann, 2000).

In a subsequent step, all models performing worse than the null model were discarded, and we calculated the average model and the averaged parameter estimates, weighted by the corrected $w_i$ values. Finally, the average model for each fauna group was used for spatial prediction of species richness in the complete study area. This information was then used to determine the priority areas for biodiversity conservation in Porto.

All models were fit using Generalized Linear Models (GLMs) in R, version 4.2.3 (R Core Team, 2023), with the aid of the packages "AICcmodavg" (Mazerolle, 2023) and "rms" (Harrell, 2023). Species richness (for the three different animal groups) was used as the response variable in GLMs with Poisson variance and log link function (Guisan and Zimmermann, 2000; Vincent and Haworth, 1983). The code used in R for the modeling framework has been previously applied by Vicente et al. (2014) (see appendix A for the full R script).

## 3. Results

### 3.1. Species richness of birds

Bird surveys revealed a total of 40 bird species across the study area; species richness in each site varied from 6 to 24 (appendix B). The multimodel inference showed substantial model selection uncertainty, suggested by the low Akaike weights ($w_i$; Table 2). It should be noted that the large number of tested models can contribute to lower $w_i$ values.

Nevertheless, among the analyzed predictors, artificial (ABE) and vegetation (Veg) cover seem to have a larger effect on bird species richness, especially at a smaller spatial scale. Although the current land cover has a relevant impact on bird species richness (ABE2019 and Veg2019), the land cover legacy was also evident, as the different land cover types recorded for 1947 (ABE1947 and Veg1947) contribute to some of the best models (Table 2). In general, artificial land cover has a negative effect on the species richness of birds (particularly ABE2019 and ABE1947), whereas vegetation cover has a positive effect (Veg2019, Veg1947). The model regarding vegetation cover change was one of the most important, but its results can be difficult to interpret, as bird species richness seems to be positively associated with all vegetated areas, as well as areas that experienced vegetation loss. However, areas that went through a recent increase in vegetation cover (VegGain and VegDisturb) appear to have a particularly positive impact on bird species

**Table 2**
Results of information-theoretic-based model selection and multimodel inference for bird species richness, showing the number of parameters ($K$), AIC difference ($\Delta_i$), Akaike weights ($w_i$), adjusted $R^2$, predictors, and their effect on bird species richness. Only the 10 best models are shown, for complete results see appendix C.

| Model | $K$ | $\Delta_i$ | $w_i$ | adj. $R^2$ | Predictors | Effect |
|---|---|---|---|---|---|---|
| M19: Artificial cover in 1947 (fine scale) | 3 | 0 | 0.152082 | 0.235324 | ABE1947F | Negative |
| M7: Artificial cover in 2019 (fine scale) | 3 | 0.039688 | 0.149094 | 0.234169 | ABE2019F | Negative |
| M5: Vegetation cover in 2019 (fine scale) | 3 | 0.619803 | 0.111555 | 0.217284 | Veg2019F | Positive |
| M18: Vegetation cover in 1947 (coarse scale) | 3 | 1.031569 | 0.090798 | 0.205298 | Veg1947C | Positive |
| M17: Vegetation cover in 1947 (fine scale) | 3 | 1.055675 | 0.08971 | 0.204597 | Veg1947F | Positive |
| M31: Vegetation cover change (fine scale) | 6 | 1.271058 | 0.080551 | 0.36497 | Veg72yF | Positive |
| | | | | | VegDisturbF | Positive |
| | | | | | VegGainF | Positive |
| | | | | | VegLossF | Positive |
| M20: Artificial cover in 1947 (coarse scale) | 3 | 2.41604 | 0.04544 | 0.165001 | ABE1974C | Negative |
| M3: Type of vegetation cover in 2019 (fine scale) | 4 | 2.870273 | 0.036208 | 0.199652 | TRS2019F | Positive |
| | | | | | HER2019F | Positive |
| M16: Type of vegetation cover in 1947 (coarse scale) | 4 | 2.911869 | 0.035463 | 0.198411 | TRS1947C | Positive |
| | | | | | HER1947C | Positive |
| M15: Type of vegetation cover in 1947 (fine scale) | 4 | 3.088168 | 0.032471 | 0.193152 | TRS1947F | Positive |
| | | | | | HER1947F | Positive |

richness. The age of vegetation cover does not seem to have an important influence on bird species richness, nor does the presence of water elements.

### 3.2. Species richness of reptiles

During reptile surveys, four species were identified in the selected sampling sites. Species richness varied between 0 and 2; the presence of reptiles was only detected in around half of the sites (appendix B).

Despite the model selection uncertainty, current vegetation cover (Veg2019, TRS2019, and HER2019) seems to have a predominant effect on reptile species richness, especially at a coarse scale (Table 3). To a lesser degree, there seems to be an influence of past land cover at different temporal and spatial scales, with past vegetation cover (Veg1979 and Veg1947) being associated with an increase in species richness and past artificial cover (ABE1979 and ABE1947) with a decrease in species richness. Although some effects of land cover legacy (past land cover) can be discerned, the age of vegetation cover and the trend of vegetation cover evolution, as well as the presence of water, do not seem to play a significant role in shaping reptile species richness.

### 3.3. Species richness of amphibians

Amphibians are one of the rarest vertebrate groups in the city of Porto. Although five species were detected, amphibians were only present in 6 of the 43 sampling sites (appendix B). The zero-inflated data may have influenced the results of the multimodel inference, as most of the models for amphibians perform poorly in explaining the variation in species richness (high values of $\Delta_i$; Table 4).

Nevertheless, the analysis suggests that the presence of water is the most important determinant of amphibian species richness (Table 4), as would be expected; this effect is particularly noticed at a finer scale.

Besides water, vegetation cover and tree and shrub cover (TRS) also seem to have an influence; the effect of land cover legacy can be seen in this group, as past vegetation patterns contribute to some of the best models (TRS1979, HER1979, TRS1947, HER1947), but not current vegetation cover. Of the studied groups, amphibians were the only to exhibit an obviously different response to TRS and HER cover: the number of species is positively influenced by TRS cover, while it is negatively related to HER cover at multiple temporal scales and particularly at a coarser resolution.

The age of vegetation cover is also integrated into the best models for determining species richness: a higher number of amphibian species seems to be associated with older habitat patches (Veg72y, Veg4071y, TRS72y, TRS4071y), while recent patches have lower species richness (Veg039y, TRS039y). Regarding the evolution trend of the vegetation cover, the patterns are unclear, but, again, a higher number of species seems to be located in areas with more persistent tree and shrub cover (TRS72y).

### 3.4. Spatial prediction and identification of priority areas

Spatial predictions from the average models for each fauna group (after the exclusion of the worst models) are presented in Fig. 2. For birds, the average model predicts values from 12 to 20 species. The lowest values are concentrated in the city center, in the south, where artificial cover is higher and vegetation cover is lower. The highest values of predicted bird species richness are located in the periphery, especially at the western and eastern extremities. Reptiles present a similar pattern, where the central core of the study area has lower values of species richness (predicted value of zero), and the periphery is predicted to be slightly more diverse (1 or 2 species). The modeling results

**Table 3**
Results of information-theoretic-based model selection and multimodel inference for reptile species richness, showing the number of parameters ($K$), AIC difference ($\Delta_i$), Akaike weights ($w_i$), adjusted $R^2$, predictors and their effect on reptile species richness. Only the 10 best models are shown, for complete results see appendix C.

| Model | $K$ | $\Delta_i$ | $w_i$ | adj. $R^2$ | Predictors | Effect |
|---|---|---|---|---|---|---|
| M6: Vegetation cover in 2019 (coarse scale) | 3 | 0 | 0.308051 | 0.328195 | Veg2019C | Positive |
| M4: Type of vegetation cover in 2019 (coarse scale) | 4 | 2.298104 | 0.097633 | 0.31194 | TRS2019C | Positive |
| | | | | | HER2019C | Positive |
| M14: Artificial cover in 1979 (coarse scale) | 3 | 2.565197 | 0.085427 | 0.249839 | ABE1979C | Negative |
| M11: Vegetation cover in 1979 (fine scale) | 3 | 2.754337 | 0.077719 | 0.244061 | Veg1979F | Positive |
| M20: Artificial cover in 1947 (coarse scale) | 3 | 3.46306 | 0.054529 | 0.222413 | ABE1947C | Negative |
| M17: Vegetation cover in 1947 (fine scale) | 3 | 3.818592 | 0.045648 | 0.211553 | Veg1947F | Positive |
| M12: Vegetation cover in 1979 (coarse scale) | 3 | 4.239417 | 0.036987 | 0.198698 | Veg1979C | Positive |
| M19: Artificial cover in 1947 (fine scale) | 3 | 4.255886 | 0.036683 | 0.198195 | ABE1947F | Negative |
| M13: Artificial cover in 1979 (fine scale) | 3 | 4.470407 | 0.032952 | 0.191642 | ABE1979F | Negative |
| M5: Vegetation cover in 2019 (fine scale) | 3 | 4.547676 | 0.031704 | 0.189282 | Veg2019F | Positive |

**Table 4**
Results of information-theoretic-based model selection and multimodel inference for amphibian species richness, showing the number of parameters ($K$), AIC difference ($\Delta_i$), Akaike weights ($w_i$), adjusted $R^2$, predictors and their effect on amphibian species richness. Only the 10 best models are shown, for complete results see appendix C.

| Model | $K$ | $\Delta_i$ | $w_i$ | adj. $R^2$ | Predictors | Effect |
|---|---|---|---|---|---|---|
| M1: Water (fine scale) | 3 | 0 | 0.738084 | 0.396837 | WaterF | Positive |
| M25: Age of vegetation cover (fine scale) | 5 | 3.82287 | 0.109139 | 0.389546 | Veg72yF | Positive |
| | | | | | Veg4071yF | Positive |
| | | | | | Veg039yF | Negative |
| M10: Type of vegetation cover in 1979 (coarse scale) | 4 | 6.361833 | 0.030666 | 0.281446 | TRS1979C | Positive |
| | | | | | HER1979C | Negative |
| M28: Tree and shrub cover change (coarse scale) | 6 | 6.819777 | 0.02439 | 0.362315 | TRS72yC | Positive |
| | | | | | TRSDisturbC | Negative |
| | | | | | TRSGainC | Positive |
| | | | | | TRSLossC | Negative |
| M2: Water (coarse scale) | 3 | 7.354496 | 0.018668 | 0.218965 | WaterC | Positive |
| M22: Age of tree and shrub cover (coarse scale) | 5 | 7.692374 | 0.015766 | 0.291161 | TRS72yC | Positive |
| | | | | | TRS4071yC | Positive |
| | | | | | TRS039yC | Negative |
| M9: Type of vegetation cover in 1979 (fine scale) | 4 | 8.134968 | 0.012636 | 0.23749 | TRS1979F | Positive |
| | | | | | HER1979F | Positive |
| M31: Vegetation cover change (fine scale) | 6 | 8.310177 | 0.011576 | 0.323423 | Veg72yF | Positive |
| | | | | | VegDisturbF | Negative |
| | | | | | VegGainF | Positive |
| | | | | | VegLossF | Positive |
| M16: Type of vegetation cover in 1947 (coarse scale) | 4 | 9.115074 | 0.007741 | 0.213193 | TRS1947C | Positive |
| | | | | | HER1947C | Negative |

show a particularly unfavorable scenario for amphibians since most of the city is predicted to have zero species, with only a few isolated squares portraying the presence of one species.

The results of the multimodel inference and the spatial predictions were used to evaluate the priority level for the entire study area regarding the conservation of urban biodiversity, according to the criteria presented in Table 5. This approach favors sites with the highest number of species (predicted or observed) for all analyzed groups, as can be seen in Fig. 3.

## 4. Discussion

### 4.1. Species richness of birds

Bird species richness in Porto seems to exhibit a positive relation with vegetated areas and a negative relation with built-up or impervious areas, in accordance to other studies (e.g., Amaya-Espinel et al., 2019; Carbó-Ramírez and Zuria, 2011; Humphrey et al., 2023). However, the adverse effect of the artificialization of the territory appears to extend here into the past, as the areas urbanized for over 72 years tend to have fewer species (e.g., near Infante D. Henrique Square and República Square). Results also suggest a legacy effect of vegetation cover, since a higher number of species persist in or close to areas vegetated in 1947, even if a large portion of vegetation cover was lost nearby (e.g., near Francisco Sá Carneiro Square and Ramalde Sports Park).

Conversely, bird species also seem to positively respond to recent vegetation cover, highlighting their high mobility and dispersal abilities that allow them to easily colonize new habitats (Lens et al., 2002) and to quickly respond to habitat changes (Atwell et al., 2012; Audet et al., 2016). In Porto, this response is associated with the creation of new green spaces that replace previously urbanized locations (e.g., Machado de Assis Garden and Sophia's Garden) and with vegetation growth in newly urbanized areas that substituted previous agricultural fields and forest patches (e.g., near Paulo Vallada Garden and Ramalde Sports Park).

Contrary to other studies (Barth et al., 2015; Fernández-Juricic, 2000), we were not able to detect a relevant influence of the age of vegetation cover on bird species richness. The use of species richness as the response variable can mask certain factors affecting particular species, especially considering the difference in habitat suitability for specialist and generalist species (Connor et al., 2018). As often reported in urban contexts, a large portion of the sampled birds in Porto corresponds to generalist and opportunistic species (such as *Turdus merula* or *Pica pica*). Only a fraction is composed of habitat specialists (forest species, such as *Certhia brachydactyla*, or grassland species, such as *Cisticola juncidis*), which tend to be associated with particular habitat niches (Connor et al., 2018) and older vegetation patches (Nordén et al., 2014). Similarly, aquatic bird species were virtually absent from most sampled sites, which can help explain why water elements did not present a relevant influence on species richness, contradicting other studies (e.g., Mbiba et al., 2021). Habitat specialists may not contribute to a significant increase in the number of species at each site, but their presence in particular locations strengthens the species richness at the city level.

Regarding the scale of analysis, birds seem to exhibit a stronger response to predictor variables measured at finer scales. This may be due to a higher detectability of birds in sites where they nest or feed, compared to sites mainly used for dispersal, typically examined at coarser scales. Alternatively, the prevalence of generalist species on the city species pool may generate a stronger link with the fine scale, as they tend to disperse less than specialist species (Martin and Fahrig, 2018; Neuschulz et al., 2013).

Although the average model was not able to precisely predict the observed bird species richness (ranging from 6 to 24 species per site), it generated a spatial pattern that is relatively close to reality. As exposed by the model spatialization, the city center, particularly the historic/medieval part, is relatively poor in bird species, with only opportunistic bird species persisting, nesting directly in buildings (e.g., *Columba livia*, *Larus michahellis*, *Passer domesticus*), due to the lack of diverse vegetated habitats. Predicted species richness of birds is concentrated in the city's periphery, where most large vegetation patches occur (e.g., City Park, Serralves Park, Prelada Park, Oriental Park, and the areas of Ervilheira/Nevogilde, Asprela, Contumil/Currais, Rio Tinto and Rio Torto). The peripheral arc was almost completely rural and semi-natural from 1947 to 1979, while the city center was already covered by a dense urban fabric in 1947.

### 4.2. Species richness of reptiles

The city of Porto harbors relatively few species of reptiles; the wall

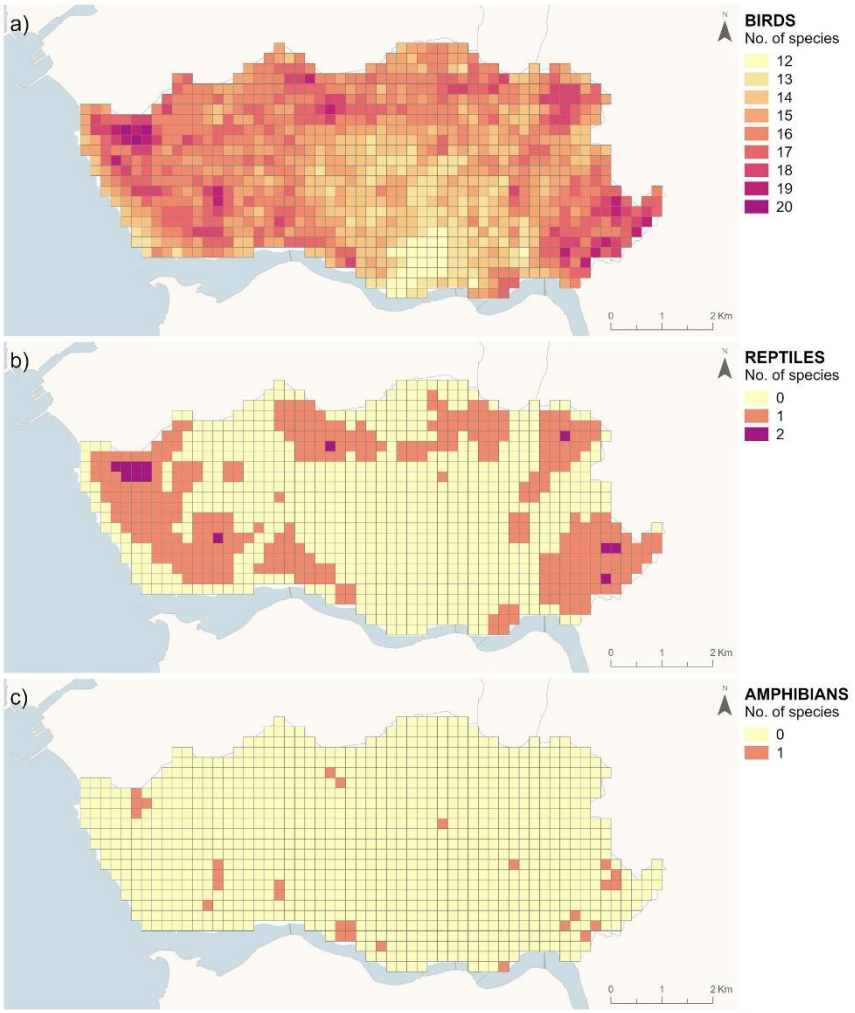



**Fig. 2.** Spatial prediction for the species richness of birds (a), reptiles (b), and amphibians (c), obtained from the average models.

**Table 5**
Criteria for the determination of the priority level according to values of species richness (observed values for sampled squares, predicted values for unsampled sites).

| Priority level | Species richness criteria | | | | |
|---|---|---|---|---|---|
| | Amphibians | | Reptiles | | Birds |
| Top priority | ≥ 1 | or | ≥ 2 | or | ≥ 19 |
| High priority | 0 | and | 1 | and | 17–18 |
| Medium priority | 0 | and | 1 | and | ≤ 16 |
| | 0 | and | 0 | and | 17–18 |
| Low priority | 0 | and | 0 | and | ≤ 16 |

lizard (*Podarcis bocagei*) is the most prevalent throughout the study area, while others occur only in isolated locations scattered throughout the territory. The low abundance and diversity of this vertebrate group, along with the generic habitat requirements of the most common species, could help explain the modest performance of most models ($\Delta_i >$ 2). Nevertheless, the modeling framework reveals interesting patterns of reptile distribution within the city (Ackley et al., 2015; García-París and Martín, 1987; Rugiero et al., 2020).

Regarding scale of analysis, the prevalence of *P. bocagei* seems to influence modeling results, as this species' generalist habits and resilience to fragmentation (Galán, 2015) may result in a stronger relationship with coarser scales. Particularly at this scale, current vegetation cover is highlighted as the most relevant factor influencing reptile species richness in Porto, aligning with other studies (e.g., De Solan et al., 2019; Vignoli et al., 2009). The results also suggest that reptiles benefit from both wooded and herbaceous habitats, which provide diverse ecological conditions necessary for foraging, basking, predator avoidance, egg-laying, and overwintering (Pulsford et al., 2018). In Porto, some locations balance tree/shrub cover and herbaceous cover, apparently benefiting reptiles (e.g., Quinta de Bonjóia, Nova Sintra Park, Pasteleira Park, Asprela area).

Although current land cover seems fundamental for reptile distribution, past land cover seems to also play an important role: higher

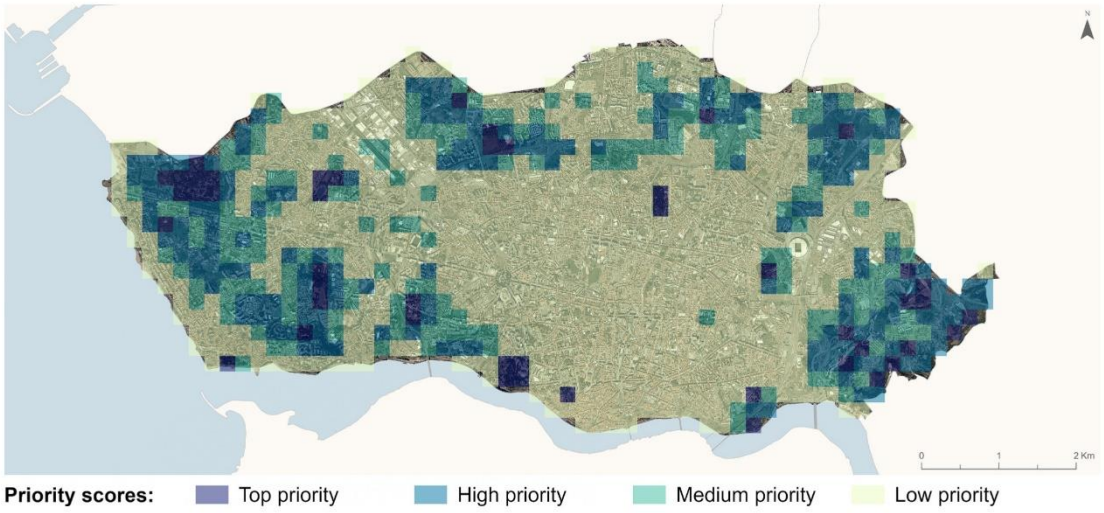



**Fig. 3.** Priority areas for the conservation of urban biodiversity in Porto, based on the effects of land cover evolution on species richness (background imagery: Direção Geral do Território, 2018).

species richness occurs in areas extensively vegetated both in 1979 and 1947, even if that vegetation was substantially reduced recently (e.g., in Amial, Areosa, and Senhora de Campanhã). This can indicate a phenomenon of extinction debt (Figueiredo et al., 2019; Kuussaari et al., 2009), where species temporarily persist in smaller patches following habitat loss and fragmentation. The response to artificial areas also seems dependent on a time scale, as areas urbanized for over 40 years displayed lower reptile occurrence and richness, while the recently built-up areas do not seem to have a significant impact. Due to this delayed response, population decline could be reverted with improved habitat quality and strengthened connectivity with source populations.

The predicted species richness distribution shows an arc-shaped pattern of reptile occurrence in the city's periphery, with reptiles seemingly excluded from the city center. The dominance of *P. bocagei* in Porto seems to influence the predicted spatial distributions of reptiles. Despite models pointing to the importance of past vegetation cover, spatial predictions of the average model failed to capture reptile persistence in smaller habitat patches associated with older vegetation patches. Most of these (e.g., in Amial, Areosa, and Senhora de Campanhã) have recently experienced habitat loss and fragmentation, retaining only a fraction of the historic habitat cover and composition. This raises concern about future local extinction of the dwindling *P. bocagei* populations at these sites, as occurred recently in other locations in Porto (authors' unpublished data).

### 4.3. Species richness of amphibians

The low species richness and low rate of occurrence of amphibians greatly conditioned the performance of the modeling framework (most models have $\Delta_i > 6$), but our results can help unveil the history of the amphibian populations of Porto.

As expected, the presence of water elements seems to be a core determinant of the occurrence of amphibian species, but other factors must be considered. Almost half of the sampled squares (19 in 43 sites) had water elements, but only six were occupied by amphibians, which could indicate unsuitable aquatic habitats, poor upland habitat quality or availability, or isolation. Many water elements in Porto's green spaces, such as tanks and fountains, are small, artificialized, have steep margins or walls, lack aquatic vegetation, and some are populated by fish, being detrimental for amphibians (Cruz et al., 2015; Fuyuki et al., 2014; Hamer et al., 2011; Parris, 2006).

Amphibian species in Porto seem to favor areas with older vegetation patches, especially those with arboreal cover in 1979, showing a positive effect similar to Piha et al. (2007) and Busby et al. (2022) for historic forests. Older green spaces, like the Botanical Garden, Virtudes Garden, Nova Sintra Park, or Covelo Park, still retain some small amphibian populations, possibly due to maintaining a high habitat heterogeneity and quality, a legacy from their past as recreational farms in the 19th century. Other older green spaces (e.g., Arca d'Água Garden, Passeio Alegre Garden, Carregal Garden), despite having a similar vegetation structure and composition, do not support amphibians as they lack suitable water features. Similarly, the modeling results suggest a negative relation between amphibians and recent vegetation patches, which present a lesser developed vegetation structure and/or no adequate aquatic habitats (e.g., José Roquette Garden, Sophia's Garden). These results may, therefore, arise from the combination of the predominance of adequate aquatic habitats and complex vegetation structures only in older parks with the limited abilities of this group for dispersal and colonization of newer green spaces (Busby et al., 2022).

The models also seem to point to a negative association between amphibians and historical herbaceous cover (1979 and 1947), possibly indicating a time-lagged response to former agricultural areas (Piha et al., 2007). On the other hand, the areas with herbaceous vegetation in 1979 and 1947, were prioritized for urbanization, which could reflect a negative response to built-up or impervious cover, as reported by several authors (e.g., Guderyahn et al., 2016; Villaseñor et al., 2017).

Despite the low model performance, the predicted spatial pattern of amphibian occurrence seems to be relatively accurate, but fails to predict values above one species, as observed in Botanical Garden and Virtudes Garden (3 species in each site). Overall, amphibians seem to be concentrated in very few isolated locations; besides the sampled sites, the modeling results seem to correctly predict the occurrence of amphibian species in other locations, such as the City Park, Serralves Park, Prelada Park, Palácio de Cristal Gardens, São Roque Park, or Oriental Park, as demonstrated by previous studies (authors' unpublished data; Pereira, 2011; Ribeiro, 2011). This severely discontinuous distribution may indicate a delayed response to habitat loss and fragmentation, where amphibians are not able to cross the inhospitable

urban matrix and become "trapped" in extremely reduced habitat patches. The modeling results appear to support the sedentary profile of amphibians and emphasize the importance of small habitat patches (even if isolated), as fine-scale models outperformed coarse-scale models (Öckinger et al., 2009).

### 4.4. Implications for urban planning and urban biodiversity conservation

At first glance, the future does not look promising for the preservation of urban biodiversity in Porto, as two-thirds of the city is covered by built-up and impervious surfaces (Guilherme et al., 2022). However, vertebrate diversity in Porto remains noteworthy, with 70 % of regional amphibian species, 54 % of regional reptile species, and 23 % of regional bird species (Farinha-Marques et al., 2023; Guilherme et al., 2015).

All studied fauna groups seem to respond to past land cover or land cover legacy – the oldest vegetation patches tend to host more species, while older urban areas are less biodiverse. The more biodiverse green spaces are 19th-century parks and gardens (e.g., Passeio Alegre Garden, Palácio de Cristal Gardens) and recent public parks that originated from recreational farms, agricultural and forest land (e.g., City Park, Serralves Park, Covelo Park, Oriental Park). Their status as public green spaces has led to the preservation, protection and promotion of habitat, flora, and fauna diversity; the same does not apply to the substantial proportion of undeveloped land that has, nonetheless, sustained its vegetation cover for over 72 years. Older and stable habitat patches foster a complex vegetation structure and diverse habitat niches, which enhances their biodiversity (Janssen et al., 2017; Nordén et al., 2014), especially for specialist, long-lived, and/or dispersal-limited species (Lira et al., 2019). As such, to maintain a higher species richness at the city level, it is essential to preserve the parks and gardens, as well as the undeveloped land, to the possible extent – the conservation of habitats in Ervilheira/Nevogilde, Prelada/Viso, Asprela, Contumil/Currais, Rio Tinto and Rio Torto seems to be particularly imperative, due to their city-wide relevance and the pressure to urbanize them (Buonincontri et al., 2023; Guilherme et al., 2024). If, or when, these spaces are urbanized, it is fundamental to preserve large patches of continuous vegetation, that could act as habitat and dispersion corridors. To complement habitat preservation and counteract the habitat loss at the city scale, it is also important to regenerate or create new habitats near older vegetation patches, as it facilitates dispersal and colonization of new green spaces, vital for species with limited dispersion abilities. Birds, being highly mobile, seem to respond positively to recent vegetation cover, unlike less mobile species such as amphibians and reptiles that face more challenges when transversing the urban matrix.

Besides preserving older habitats and creating new ones, the options for the design, composition, and maintenance, of both existing and future green spaces, should be conducive to high biodiversity levels. Green spaces should incorporate a combination of woodlands, clearings, and multiple vertical layers of vegetation, along with specific microhabitat elements in strategic locations, such as water elements for amphibians, refuges for reptiles, nest boxes for birds, plant species associated with fauna species, etc. This could be decisive for the conservation of rare or specialist species, as well as common species struggling in dense urban environments (Jokimäki et al., 2018).

Amphibians can be considered the most vulnerable vertebrate group in Porto, for which conservation measures are most pressing. They are highly susceptible to fragmentation, but are able to maintain precarious populations in small habitat patches if the habitat requirements are met (Ribeiro et al., 2009b). The preservation of the few parks and gardens where amphibians occur (e.g., City Park, Serralves Park, Pasteleira Park, Botanical Garden, Palácio de Cristal Gardens, Virtudes Garden, Prelada Park, Covelo Park, S. Roque Park, Nova Sintra Park, and Oriental Park) would also have an "umbrella effect" on other vertebrates. In other green areas with adequate upland habitats, but where amphibians currently do not occur (e.g., Palácio de Cristal Gardens), we recommend implementing adequate water features suitable for reproduction or improving the existing ones. These measures should be complemented with the creation of strategic green corridors, especially in the northern peripherical arc, along the bank of the River Douro, and in the western section of the city. This would facilitate amphibian dispersal through the urban fabric, promoting the colonization of new areas and maintaining a greater genetic diversity in existing populations (Velo-Antón et al., 2021).

Reptiles are also rather scarce in Porto, but the most common species is quite resistant to fragmentation and able to persist in urbanized areas with reduced vegetation. Other species face challenges finding suitable habitats and are sensitive to fragmentation. To promote reptile presence, recommended measures involve guaranteeing diverse microhabitats in remaining vegetated areas (Croci et al., 2008), focusing on places for refuge or shelter for target species. Given reptiles' reduced dispersal, it is crucial to reinforce the connectivity between green spaces and to create new green spaces to function as stepping stones.

Birds are the most successful group of vertebrates in Porto, with even early urbanized areas presenting interesting levels of species richness. However, this diversity often stems from commensal, opportunistic and/or exotic species, particularly in the city center. To balance this situation, the presence of specialist and rare species should be encouraged by diversifying habitat niches in strategic locations, as current green areas have a simplified vegetation structure and composition, only benefiting a restricted number of species. Recommendations include installing nest boxes for cavity-nesting birds and emphasizing shrub and herbaceous layers to complement trees. Since birds seem to positively respond to recent habitat transformation and can overcome isolation caused by the urban matrix, we recommend the multiplication and enlargement of green spaces, mainly towards the biologically impoverished city center. These measures could deliver quick results even in scenarios of lower physical connectivity (Evans et al., 2009).

### 4.5. Limitations and future research

For this study, we intended to understand the response of different fauna groups to the land cover evolution in Porto, in the close historical past for which there is remote sensing data. Although this was not possible due to limited resources and lack of available data, we recommend using shorter time intervals to better capture the fast-paced dynamics of urban areas and the biodiversity response to these dynamics. Other limitation was the reduced number of records of species occurrences, either within the study area or in the surroundings. If sufficient records were available, model of species occupancies could be produced and, subsequently, potential species richness could be estimated (Ribeiro et al., 2009a). Lacking this information, species richness had to be calculated from current individual data on each species. While already expected, due to the biological impoverishment of urban areas that is detrimental to species abundance and diversity, the excess of "zeros" had repercussions in the statistical analysis. Primarily, as indicated by the values of AIC and $\Delta_I$, it affected the robustness of most of the models. Despite the low statistical support, the modeling results and the spatial predictions reveal interesting tendencies and patterns that line up with our previous knowledge about vertebrate species distribution in the city of Porto. Additionally, we were not able to test complex interactions among variables, as they can be challenging to implement in a multimodel inference framework. The evaluation of interactions is limited to variables present in a specific model and interactions might occur between variables not shared within the same model. As each model relates to a different hypothesis, this could lead to confounding effects when testing among competing hypotheses. We argue that, while not strictly required for testing our primary hypotheses, interactions could enhance the fit of certain models and help support some of them; this should be a research focus for the near future.

We acknowledge that for decision-making on the preservation and regeneration of habitats at the city scale, as well as their design and management at the local scale, information on site species richness may

not be sufficient. For future research on the influence of land use legacy on urban biodiversity, a functional ecology perspective could be valuable to provide a more accurate portrayal of the relationship. It would be beneficial to know the species composition of communities, the species diversity at larger scales, and identify priority species for conservation. As a general rule, the most sensitive species, those with greater ecological specificities, or those with a more restricted distribution, should be prioritized.

## 5. Conclusions and recommendations

In conclusion, our research of vertebrate biodiversity in the city of Porto has provided valuable insights into the complex interplay between land cover evolution and the species richness distribution of birds, reptiles, and amphibians. Birds, with their higher diversity, mobility, and adaptability, are able to thrive in a broader range of habitats, including new green spaces and areas with recent vegetation cover, which underscores the importance of urban planning that prioritizes the preservation and regeneration of older habitats, as well as the creation of new ones in previously urbanized areas. This brings hope to the promotion of biodiversity in the city center, which is currently biologically impoverished, as birds present a high probability to colonize new habitat patches, even with low physical connectivity, if the right local habitat requirements are met. Since the bird species pool in Porto is rather diverse, we recommend the provision of diverse vegetation layers and nesting structures.

Amphibians and reptiles, on the other hand, face more challenges in urban environments, with only a few species able to adapt to the heavily urbanized areas of Porto. Reptiles have been able to persist mostly in the peripheral arc, where green spaces are more abundant. Our study highlights the need for maintaining a diverse matrix of vegetation and habitats, ensuring the presence of suitable microhabitats, and strengthening connectivity between urban green spaces, as well as nearby semi-natural habitats, to support reptile populations. Amphibians, with their limited mobility, are particularly vulnerable to habitat fragmentation, and their occurrence in Porto is essentially concentrated in older parks and gardens. To safeguard both groups, it is crucial to preserve and enhance the quality of green spaces, implement water features suitable for amphibians, and establish strategic green corridors to facilitate dispersal.

While urbanization continues to expand, efforts must be made to strike a balance between urban development and biodiversity preservation, which should be considered in the multiple stages of urban planning, design, and management. This involves not only conserving older habitats, but also creating new ones, even in areas where urbanization is to occur, fostering diverse vegetation and microhabitats, and prioritizing the most sensitive and specialist species. By implementing these recommendations, Porto can work towards preserving and improving its biodiversity and ensuring a sustainable coexistence between its human and natural inhabitants. This study serves as a valuable resource for decision-makers, urban planners, and conservationists in their efforts to create a more ecologically resilient and biodiverse city.

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## CRediT authorship contribution statement

**Filipa Guilherme:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Joana R. Vicente:** Formal analysis, Methodology, Writing – review & editing. **Miguel A. Carretero:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing. **Paulo Farinha-Marques:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing.

## 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.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

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# Article III. R script

Example of the R script used to perform the multimodel inference regarding the species richness of birds.

```
##############################################################################################
MAPPING MULTIGROUP RESPONSES TO LAND COVER LEGACY FOR URBAN BIODIVERSITY CONSERVATION
in Biological Conservation (2024)
##############################################################################################

library(AICcmodavg)

setwd("C:/Users/...")

## Input tables
inputdata<-read.table("bird_vars.txt",h=T,sep="\t")
library(rms)


#++++++++++++++

modelsdf<-read.table("modelset.txt",h=T,sep="\t",row.names="Model")

inputdata$V0<-runif(nrow(inputdata)) #add a random noise variable
inputdata<-subset(inputdata,   select=c("birdSRt",   "WaterF",   "WaterC",   "TRS2019F",
"HER2019F",  "TRS2019C",  "HER2019C",  "Veg2019F",  "Veg2019C",  "ABE2019F",  "ABE2019C",
"TRS1979F",  "HER1979F",  "TRS1979C",  "HER1979C",  "Veg1979F",  "Veg1979C",  "ABE1979F",
"ABE1979C",  "TRS1947F",  "HER1947F",  "TRS1947C",  "HER1947C",  "Veg1947F",  "Veg1947C",
"ABE1947F",  "ABE1947C",  "TRS72yF",  "TRS4071yF",  "TRS039yF",  "TRS72yC",  "TRS4071yC",
"TRS039yC",  "HER72yF",  "HER4071yF",  "HER039yF",  "HER72yC",  "HER4071yC",  "HER039yC",
"Veg72yF", "Veg4071yF", "Veg039yF", "Veg72yC", "Veg4071yC", "Veg039yC", "TRSDisturbF",
"TRSGainF", "TRSLossF", "TRSDisturbC", "TRSGainC", "TRSLossC", "HERDisturbF", "HERGainF",
"HERLossF",   "HERDisturbC",   "HERGainC",   "VegDisturbF",   "VegGainF",   "VegLossF",
"VegDisturbC", "VegGainC", "VegLossC", "V0"))

#++++++++++++++


########################################
## Returns the index of a given value ##
########################################

get.index <- function(x, value){
        x.sel<-x==value
        x.indexes<-1:length(x)
        return(x.indexes[x.sel])
}

#################
## Adjusted D2 ##
#################

adj.d2<-function(glmobj){
```

```
          go<-glmobj
          D2<-(go$null.deviance-go$deviance)/go$null.deviance
          p<-length(go$coefficients)
          n<-length(go$fitted)
          adj.D2<-1-((n-1)/(n-p))*(1-D2)
          return(adj.D2)
}

d2 <- function(glmobj){
          return(1-(glmobj$deviance/glmobj$null.deviance))
}

#####################################################################
## Assembles a formula using the dataset header to name variables ##
#####################################################################

# Uses the column position/index

formula.assemble<-
function(data,var.dependent,var.predictors,transf.function=NULL,parameters.str=NULL){
          var.names<-colnames(data)
          var.n<-length(var.names)

          if(length(var.dependent)!=1) stop("The parameter var.dependent should contain
only the column index of the dependent variable!")
          form<-as.character(paste(var.names[var.dependent],"~"))
          k<-0

          # Two basic working modes: "all" extracts all variables in the dataset except
the dependent; or a user defined (sub-)set
          ## All predictors mode
          if(as.character(var.predictors[1])=="all"){
               for(i in 1:var.n){
                 if(i==var.dependent)
                      next
                 else{
                      k<-k+1
                      if(is.null(transf.function)==FALSE                                &&
is.null(parametepoissonrs.str)==FALSE && is.factor(data[,i])==FALSE){
                        form               <-               paste(form,if(k!=(var.n-1))
paste(transf.function,"(",var.names[i],",",parameters.str,") + ")
                                                           else
paste(transf.function,"(",var.names[i],",",parameters.str,")"))
                      }
                      else{
                        form <- paste(form,if(k!=(var.n-1)) paste(var.names[i]," + ")
                                                           else paste(var.names[i]))
                      }
                 }
               }
          }
          ## Selected predictors only
          else{
               for(i in 1:length(var.predictors)){
                 k<-k+1
                 if(is.null(transf.function)==FALSE && is.null(parameters.str)==FALSE &&
is.factor(data[,i])==FALSE){
```

```
                    form      <-      paste(form,      if(k!=length(var.predictors))
paste(transf.function,"(",var.names[var.predictors[i]],",",parameters.str,") + ")
                                                       else
paste(transf.function,"(",var.names[var.predictors[i]],",",parameters.str,")"))
                }
                else{
                    form      <-      paste(form,      if(k!=length(var.predictors))
paste(var.names[var.predictors[i]]," + ")
                                                       else
paste(var.names[var.predictors[i]]))
                }
              }
         }
         return(as.formula(form))
}

############################
## AIC weights calculation ##
############################

## By default uses the dependent variable in the first column

Modav.AICc<-
function(modelsdf,inputdata,transf.func=NULL,param=NULL,model.family=poisson,glm.model.w
eights=NULL){

              outdata<-data.frame()
              glm.model.weights<<-glm.model.weights
              res<-list()

              for(i in 1:nrow(modelsdf)){

                tmp.modelsdf<-data.matrix(modelsdf)
                tmp.vcols<- get.index(tmp.modelsdf[i,],1)+1
                tmp.form<-
formula.assemble(inputdata,var.dependent=1,var.predictors=tmp.vcols,transf.function=tran
sf.func,parameters.str=param)
                tmp.glm<-
glm(tmp.form,data=inputdata,family=model.family,weights=glm.model.weights)
                res[[paste("glm",i,sep="_")]]<-tmp.glm

                P<-length(coef(tmp.glm))+1

                outdata[i,"npar"]<-length(coef(tmp.glm))+1

                #outdata[i,"logL"]<-tmp.glm$deviance/2
                outdata[i,"logL"] <- logLik(tmp.glm)

                #outdata[i,"AICc"]<-
tmp.glm$deviance+2*P+(2*P*(P+1)/(2*sum(inputdata[1])-P-1))
                outdata[i,"AICc"]<-AICcmodavg::AICc(tmp.glm)

                outdata[i, "adj.D2"]<-adj.d2(tmp.glm)

                # Adds Spearman correlation
                outdata[i,"Cor.Sp"]<-
cor(tmp.glm$y,tmp.glm$fitted.values,method="spearman")
```

```
                # Intercept term
                outdata[i,"Ipt"]<-coef(tmp.glm)[1]

                ## Without tranformation
                if(is.null(transf.func)==TRUE || is.null(param)==TRUE){
                      for(j in 2:ncol(inputdata)){

                        tmp.name<-names(inputdata)[j]
                        tmp.vec<-tmp.name==names(coef(tmp.glm)[-1])
                        tmp.pos<-get.index(tmp.vec,TRUE)

                        if(sum(tmp.vec)==1)             outdata[i,names(inputdata)[j]]<-
(coef(tmp.glm)[-1])[tmp.pos]
                        else outdata[i,names(inputdata)[j]]<-0
                      }
                }
                ## Supports Designs' pol() transformation
                else if(transf.func=="pol" || is.null(param)==FALSE){
                      data.col.names<-colnames(inputdata)[-1]
                      transf.col.names<-vector()

                      for(k in 1:length(data.col.names)){
                        if(k==1){
                              transf.col.names[1]<-
paste(transf.func,"(",data.col.names[k],", ",param,")",data.col.names[k],sep="")
                              transf.col.names<-
c(transf.col.names,paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],"^2",sep=""))
                        }
                        else{
                              transf.col.names<-
c(transf.col.names,paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],sep=""))
                              transf.col.names<-
c(transf.col.names,paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],"^2",sep=""))
                        }
                      }

                      for(k in 1:length(transf.col.names)){
                        tmp.name<-transf.col.names[k]
                        tmp.vec<-tmp.name==names(coef(tmp.glm)[-1])
                        tmp.pos<-get.index(tmp.vec,TRUE)

                        if(sum(tmp.vec)==1)             outdata[i,transf.col.names[k]]<-
(coef(tmp.glm)[-1])[tmp.pos]
                        else outdata[i,transf.col.names[k]]<-0
                      }
                }
                else stop("Non-supported transformation!")
              }

          outdata[,"deltaAICc"]<-outdata$AIC-min(outdata$AICc)
          outdata[,"winumer"]<-exp(-0.5*outdata$deltaAICc)
          outdata[,"wi"]<-outdata$winumer/sum(outdata$winumer)
```

```
          i<-6 # This number was changed to accomodate both the adj.D2 and the Cor.Sp
columns
          outvec<-vector(length=dim(outdata)[2]-10)

          while(i<=(dim(outdata)[2]-3)){
                outvec[i]<-sum(outdata[,i]*outdata$wi)
                i<-i+1
          }

          res[["outdata"]]<-outdata
          res[["outvec"]]<-as.data.frame(outvec[-(1:5)]) # Altered / remove performance
indicators (npar, logL, AICc, adj.D2, Cor.Sp)

          if(is.null(transf.func)==TRUE                    ||          is.null(param)==TRUE)
rownames(res[["outvec"]])<-c("Intercept",colnames(inputdata)[-1])
          else rownames(res[["outvec"]])<-c("Intercept",transf.col.names)

          return(res)
}

###################
## MMI Framework ##
###################

## By default uses the dependent variable in the first column

Modav.var<-
function(modelsdf,inputdata,transf.func=NULL,param=NULL,glm.model.family=poisson,glm.mod
el.weights=NULL,outdataAICw){

          glm.model.weights<<-glm.model.weights
          SE1<-data.frame()
          SE2<-data.frame()
          SE3<-data.frame()
          SE4<-data.frame()
          SE5<-vector()

          for(i in 1:nrow(modelsdf)){

                tmp.modelsdf<-data.matrix(modelsdf)
                tmp.vcols<-get.index(tmp.modelsdf[i,],1)+1
                tmp.form<-formula.assemble(inputdata,
var.dependent=1,var.predictors=tmp.vcols,transf.function=transf.func,parameters.str=para
m)
                tmp.glm<-
glm(tmp.form,data=inputdata,family=glm.model.family,weights=glm.model.weights)

                SE1[i,"Ipt"]<-data.frame(coef(summary(tmp.glm)))$Std..Error[1]

                if(is.null(transf.func)==TRUE || is.null(param)==TRUE){
                  for(j in 2:ncol(inputdata)){
                        tmp.name<-names(inputdata)[j]
                        tmp.vec<-tmp.name==names(coef(tmp.glm)[-1])
                        tmp.pos<-get.index(tmp.vec,TRUE)
                        if(sum(tmp.vec)==1)                    SE1[i,names(inputdata)[j]]<-
(data.frame(coefficients(summary(tmp.glm)))$Std..Error[-1])[tmp.pos]
```

```
                    else SE1[i,names(inputdata)[j]]<-0
                }
              }
              else if(transf.func=="pol" && is.null(param)==FALSE){
                data.col.names<-colnames(inputdata)[-1]
                transf.col.names<-vector()

                for(k in 1:length(data.col.names)){
                    if(k==1){
                      transf.col.names[1]<-paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],sep="")
                      transf.col.names<-
c(transf.col.names,paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],"^2",sep=""))
                    }
                    else{
                      transf.col.names<-
c(transf.col.names,paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],sep=""))
                      transf.col.names<-
c(transf.col.names,paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],"^2",sep=""))
                    }
                }

                for(k in 1:length(transf.col.names)){
                    tmp.name<-transf.col.names[k]
                    tmp.vec<-tmp.name==names(coef(tmp.glm)[-1])
                    tmp.pos<-get.index(tmp.vec,TRUE)
                    if(sum(tmp.vec)==1)                    SE1[i,transf.col.names[k]]<-
(data.frame(coefficients(summary(tmp.glm)))$Std..Error[-1])[tmp.pos]
                    else SE1[i,transf.col.names[k]]<-0
                }
              }
              else stop("Non-supported transformation!")
        }

        SE1<-nrow(SE1)*SE1^2

        for(i in 1:nrow(modelsdf)){

              # Starts the formula with the response variable
              tmp.modelsdf<-data.matrix(modelsdf)
              tmp.vcols<-get.index(tmp.modelsdf[i,],1)+1
              tmp.form<-formula.assemble(inputdata,
var.dependent=1,var.predictors=tmp.vcols,transf.function=transf.func,parameters.str=para
m)
              tmp.glm<-
glm(tmp.form,data=inputdata,family=glm.model.family,weights=glm.model.weights)

              SE2[i,"Ipt"]<-coef(tmp.glm)[1]

              if(is.null(transf.func)==TRUE || is.null(param)==TRUE){
                for(j in 2:ncol(inputdata)){
                    tmp.name<-names(inputdata)[j]
                    tmp.vec<-tmp.name == names(coef(tmp.glm)[-1])
                    tmp.pos<-get.index(tmp.vec,1)
```

```
                    if(sum(tmp.vec)==1)   SE2[i,names(inputdata)[j]]<-(coef(tmp.glm)[-
1])[tmp.pos]
                    else SE2[i,names(inputdata)[j]]<-0
                  }
                }
                else if(transf.func=="pol" && is.null(param)==FALSE){
                  data.col.names<-colnames(inputdata)[-1]
                  transf.col.names<-vector()

                  # Generates the coefficients names in the model
                  for(k in 1:length(data.col.names)){
                    if(k==1){
                      transf.col.names[1]<-paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],sep="")
                      transf.col.names<-
c(transf.col.names,paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],"^2",sep=""))
                    }
                    else{
                      transf.col.names<-
c(transf.col.names,paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],sep=""))
                      transf.col.names<-
c(transf.col.names,paste(transf.func,"(",data.col.names[k],",
",param,")",data.col.names[k],"^2",sep=""))
                    }
                  }

                  for(k in 1:length(transf.col.names)){
                    tmp.name<-transf.col.names[k]
                    tmp.vec<-tmp.name==names(coef(tmp.glm)[-1])
                    tmp.pos<-get.index(tmp.vec,TRUE)
                    if(sum(tmp.vec)==1)                  SE2[i,transf.col.names[k]]<-
(data.frame(coefficients(summary(tmp.glm)))$Std..Error[-1])[tmp.pos]
                    else SE2[i,transf.col.names[k]]<-0
                  }
                }
                else stop("Non-supported transformation!")
          }

          i<-1
          for (i in 1:nrow(SE2)){
                SE2[i,]<-SE2[i,]*SE1
                i<-i+1
          }

          SE2<-SE2^2
          SE4<-(SE2+SE1)^1/2

          j<-1
          for(j in 1:ncol(SE4)){
                SE4[,j]<-SE4[,j]*outdataAICw$wi
                j<-j+1
          }

          i<-1
          for(i in 1:ncol(SE4)) {
```

```
            SE5[i]<-sum(SE4[,i])^2
            i<-i+1
        }
        SE5 <- as.data.frame(SE5)
        if(is.null(transf.func)==TRUE      ||   is.null(param)==TRUE)   rownames(SE5)<-
c("Intercept",colnames(inputdata)[-1])
        else rownames(SE5) <- c("Intercept",transf.col.names)
        return(SE5)
}


## Examples for Modav.AICc
Modav.AICc.obj <- Modav.AICc(modelsdf,inputdata,transf.func=NULL,param=2)

write.csv(Modav.AICc.obj$outdata,"outdata.csv")
write.csv(Modav.AICc.obj$outvec,"outvec.csv")
print(Modav.AICc.obj$outdata)
print(Modav.AICc.obj$outvec)

## Implement the model and calculate both predicted and residuals
## Extract residuals using a 'for' loop considering each model in modelsdf

nRep<-nrow(modelsdf)
tmp.rsd<-matrix(0,nrow=nrow(inputdata),ncol=nRep)
tmp.rsd.wi<-matrix(0,nrow=nrow(inputdata),ncol=nRep)

for(i in 1:nRep){
       tmp.rsd[,i]<-residuals(Modav.AICc.obj[[paste("glm",i,sep="_")]])
       tmp.rsd.wi[,i]<-
residuals(Modav.AICc.obj[[paste("glm",i,sep="_")]])*Modav.AICc.obj[["outdata"]][i,"wi"]
}

sum.abs<-function(x) sum(abs(x))
w.resid<-apply(tmp.rsd.wi,1,sum.abs)

write.csv(tmp.rsd,file="nonWeightedResiduals.csv")
write.csv(tmp.rsd.wi,file="WeightedResiduals.csv")
write.csv(w.resid,file="WSumResiduals.csv")
```