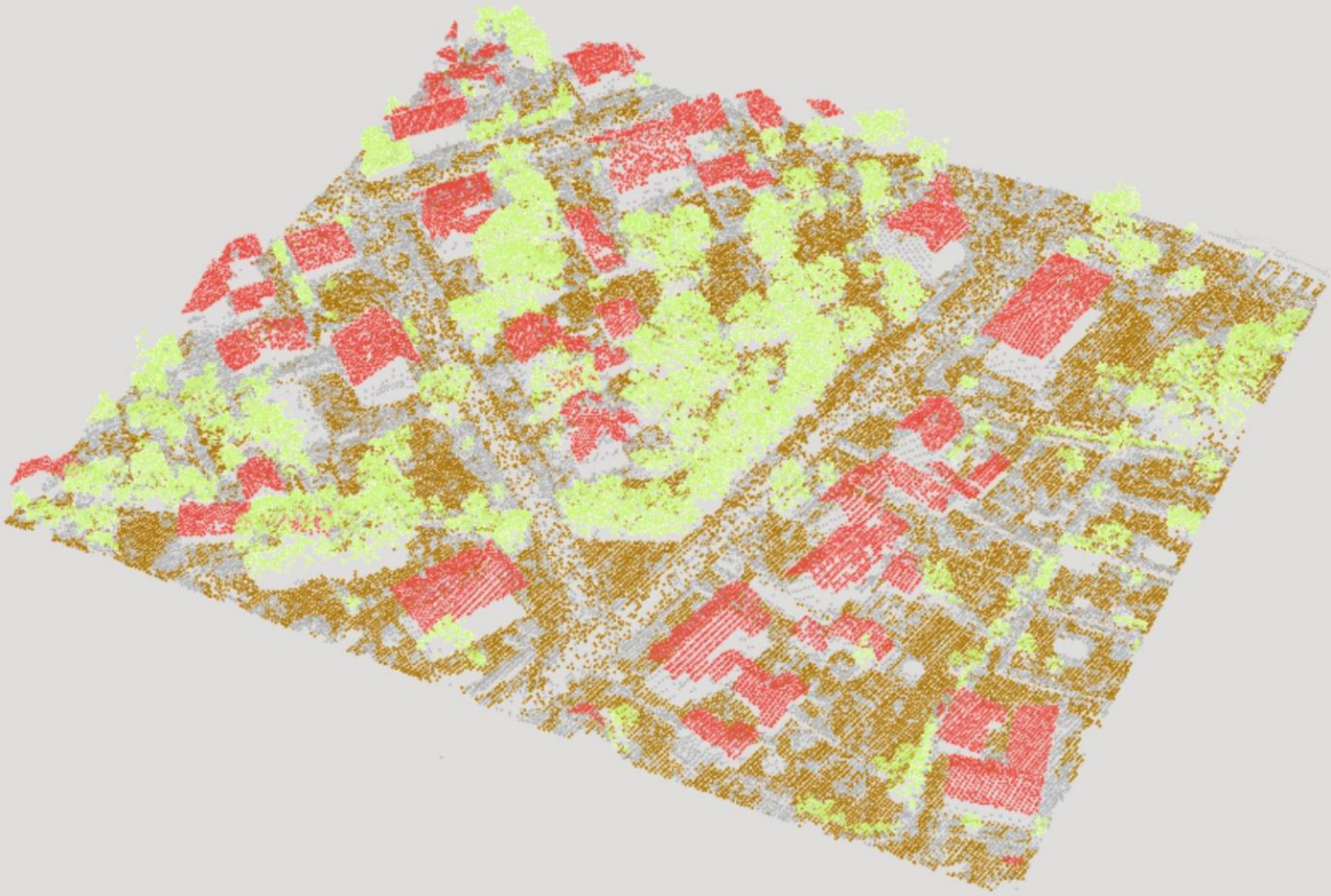
Birds in human-modified landscapes: Insights from urban and mining sites



doctoral thesis

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Birds in human-modified landscapes: Insights from urban and mining sites

Doctoral Thesis

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Declaration

I hereby declare that the dissertation entitled "Birds in human-modified Landscapes: Insights from Urban and Mining Sites" submitted for the degree of Doctor in Philosophy in the study program Applied and Landscape Ecology, is my original work guided by my supervisor. All sources of information, text, illustrations, tables, and images have been specifically cited.

Acknowledgments

I would like to thank my supervisor Petra for giving me guidance on my work and the motivation to complete it. I would also like to acknowledge all my co-authors who contributed to this thesis and all my colleagues who helped and supported me.

My greatest thanks go to my family. To my parents for always supporting me in going my own way. To my children for giving me motivation and teaching me patience. Last but not least, I would like to thank my husband Vitek for the wonderful support and help he has given me through thick and thin during the writing of this work.

Abstract

Post-mining and urban landscapes undergo substantial modification due to human activities. Mining and urban sprawl completely change original landscapes and affect entire ecosystems by altering topography, degrading soil quality, causing habitat fragmentation, changing microclimates, reducing biodiversity, and disrupting natural water flow and nutrient cycles. As mining activities and urban sprawl continue, driven by increasing human populations and the demand for resources, they further destroy original ecosystems and threaten biodiversity. Understanding the ecological processes in these altered environments is essential for designing effective conservation, restoration, and management strategies.

Birds play a crucial role in the initial colonization of newly transformed areas, including urban landscapes and areas affected by mining activities. Due to their high visibility and detectability, birds also serve as valuable bioindicators. This dissertation aims to investigate the habitat preferences of birds in human-altered environments and to provide practical guidelines for urban planning and restoration management to enhance bird species richness.

The dissertation is organized into three parts. The first part includes a preface and a theoretical background, offering an introduction to urbanization and restoration practices and their effects on (bird) diversity. The second part presents the actual research and consists of three chapters, which are conceived as independent studies. The first study compares the suitability of new and old housing developments for urban bird species and evaluates the effect it has on their population on the example of house sparrow. The second study utilizes remote sensing data to show how different methods of spoil heap reclamation affect the character of the environment and, subsequently, species richness and rarity. The third study compares the character of the environment and richness of several bird guilds with diverse nesting, foraging, and feeding behaviors on the spoil heap and its surroundings. The final part provides links among individual studies, discusses the most interesting aspects of this research, and provides insight into how the results of these studies have been used and cited.

We found that house sparrow abundance was significantly higher in older built-up areas compared to newer ones, a trend that persisted regardless of the age of the newer areas. Sufficient green space and the presence of backyard poultry were key factors contributing to house sparrow abundance. In a post-mining area, we found that spontaneously successional sites emerged as crucial for creating restored ecosystems of high ecological value, as they offer a unique combination of terrain

features, vegetation structure, and senescent vegetation that supports high bird species rarity. Furthermore, promoting a mosaic of habitats with heterogeneous vertical structure during restoration can enhance species richness. Integrating habitat heterogeneity metrics derived from airborne remote sensing data into restoration success assessment, along with repeated data acquisition, can support management interventions aiming at promoting biodiversity.

Abstrakt (Czech)

Krajina po těžbě nerostných surovin a městská krajina prochází výraznými změnami způsobenými lidskou činností. Těžba a rozrůstání měst zcela mění původní krajinu a ovlivňují celé ekosystémy tím, že mění topografii, zhoršují kvalitu půdy, způsobují fragmentaci stanovišť, mění mikroklima, snižují biologickou rozmanitost a narušují přirozený tok vody a koloběh živin. Vzhledem k pokračujícímu rozvoji těžby a urbanizace, které jsou poháněny rostoucí lidskou populací a poptávkou po zdrojích, dochází k dalšímu ničení původních ekosystémů a ohrožení biologické rozmanitosti. Pro navrhování účinných strategií ochrany, obnovy a managementu je klíčové porozumět ekologickým procesům v těchto změněných prostředích.

Ptáci hrají zásadní roli při počáteční kolonizaci přeměněných oblastí, včetně městské krajiny a lokalit ovlivněných těžbou. Díky své nápadnosti a snadné sledovatelnosti jsou také významnými bioindikátory. Cílem této disertační práce je prozkoumat habitatové preference ptáků v prostředí pozměněném lidskou činností a poskytnout praktická doporučení pro územní plánování a management obnovy oblastí ovlivněných těžbou s cílem posílit druhovou bohatost ptáků.

Disertační práce se skládá ze tří částí. První část zahrnuje předmluvu a teoretický rámec, který poskytuje úvod do urbanizace, postupů rekultivace a jejich vlivu na diverzitu ptáků. Druhá část představuje vlastní výzkum, rozdělený do tří kapitol koncipovaných jako samostatné studie. První studie porovnává vhodnost nové a staré zástavby pro městské druhy ptáků, přičemž hodnotí vliv na jejich populace na příkladu vrabce domácího. Druhá studie využívá data z dálkového průzkumu Země, aby ukázala, jak různé metody rekultivace výsypek ovlivňují charakter prostředí a následně druhovou bohatost a vzácnost. Třetí studie porovnává charakter prostředí a bohatství několika ptačích gild s rozmanitým hnízdním chováním, způsoby získávání potravy a krmení na výsypce a v jejím okolí. Závěrečná část propojuje jednotlivé studie, diskutuje nejzajímavější aspekty tohoto výzkumu a nabízí vhled do toho, jak byly výsledky těchto studií využity a citovány.

Zjistili jsme, že početnost vrabců domácích byla výrazně vyšší ve starší zástavbě ve srovnání s novou, přičemž tento rozdíl přetrvával bez ohledu na stáří nové zástavby. Mezi klíčové faktory, které přispívaly k vyšší početnosti vrabců, patřila rozloha zeleně a přítomnost drůbeže na zahradách. Na posttěžebních plochách jsme zjistili, že spontánní sukcesní stanoviště hrají zásadní roli při vytváření obnovených ekosystémů s vysokou ekologickou hodnotou, protože nabízejí jedinečnou kombinaci terénních prvků, struktury vegetace a senescentní vegetace,

která podporuje výskyt vzácných ptačích druhů. Podpora mozaiky stanovišť s heterogenní vertikální strukturou v rámci obnovy těžbou zasažených oblastí přispívá ke zvýšení druhové bohatosti.

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Chapter I – Thesis Preface

Foreword

To boldly go where no bird has gone before! Due to their high dispersal ability, birds play an important role in the initial colonization of new areas, including those that have undergone a large-scale transformation due to human intervention. Because of their high visibility and detectability, birds are often used in ecological studies as potential bioindicators. Some groups of bird species have also been proposed as „surrogates“ or proxies identifying hotspots of species richness or other measures of biodiversity. Therefore, birds are one of the best indicators for assessing the biodiversity of areas that have undergone major disturbance, such as urbanized areas or sites restored after mining.

With no doubt, urban sprawl and mining activities will persist globally, driven by increasing human populations and the demand for resources, leading to the ongoing destruction of original ecosystems. Both urbanization and mining significantly alter the landscape, causing vegetation removal and altering topography, which, in turn, leads to the fragmentation and loss of ecosystems, change in local climate conditions, and disruption of natural water cycles. Urbanization fundamentally reshapes the environment by converting natural habitats into built-up environments, such as cities, suburbs, and infrastructure networks. Dumping of waste materials resulting from mining activities on spoil heaps, on the other hand, creates barren landscapes. Spoil heaps are typically composed of rock, soil, and other by-products deposited in large mounds that bury the original landscape.

Despite the challenges related to habitat degradation and loss of biodiversity, urban areas and post-mining sites also present unique opportunities for creating new habitats. Urban landscapes can be designed to incorporate green spaces, parks, and sustainable infrastructure that not only meet human needs but also accommodate species other than humans (i.e., support biodiversity). For instance, urban areas can be designed in a way that embraces the concept of ecological urbanism, which recognizes cities as part of the natural world and suggests designing them accordingly. Similarly, the restoration of mining areas provides

opportunities to support both human activities and natural ecosystems. Through restoration efforts, these areas can be transformed into valuable wildlife habitats. Moreover, they can be designed to complement urban development, providing recreational spaces for communities and creating buffers that help mitigate environmental impacts. In this way, both urbanized areas and spoil heaps can be managed to meet human needs while also supporting the resilience and health of natural ecosystems.

However, despite good intentions, such efforts often fail to effectively benefit wildlife. This is largely due to an anthropocentric approach, where aesthetic preferences and human ideas of what constitutes a suitable habitat take precedence over the actual needs of animals. To effectively support biodiversity in altered environments, it is crucial to understand the factors that influence species diversity and distribution. In addition, employing robust monitoring methods, such as remote sensing technologies, is vital for assessing habitat conditions and changes over time. By integrating these tools, we can make informed decisions and adapt our management practices to enhance and sustain biodiversity in urban and post-mining environments.

The presented thesis explores how housing development and restoration practices influence bird species. Specifically, it investigates two key areas: First, it examines how differences in urban environment (i.e. new versus old housing areas) affect house sparrows abundance. Second, utilizing remote sensing data, including airborne laser scanning and hyperspectral imagery, it assesses the effects of habitat heterogeneity on bird diversity in restored and surrounding areas.

Research motivation

The initial spark for my ornithological research was ignited during my childhood, spent bird-watching with my grandfather. What began as a hobby evolved into a profound academic interest. Over time, I progressed to studying the behavior and ecology of individual species. At the turn of the 20th and 21st centuries, the decline of the house sparrow became widely discussed in many European countries. So, I later started to focus on this species in my bachelor's and master's thesis. By that time, the decline of the house sparrow population in farmland areas had slowly stopped, and its population had stabilized at a new, lower level. However, an even more dramatic decline was underway in urban areas, with some places

experiencing a decline of up to 90% of the original population with no obvious reasons for such a trend (e.g. De Laet & Summers-Smith 2007). Although the urban decline has been the subject of much speculation, the underlying reasons are still not properly understood.

The decline of the house sparrow has drawn general attention to birds in urban environments. Urban habitats had been largely neglected by ornithologists and it was the general public that first drew attention to the significant decline of house sparrows in city centres. During an extensive literature review, I found urban areas to constitute an interesting field of research. This area of investigation carries substantial importance, given that urban areas are growing rapidly throughout the world, and this trend is expected to continue as urban areas absorb most of the global population growth in the future.

Later, during my PhD studies and while working on my paper on the house sparrow, I began collaborating with my future husband, who was then exploring the use of lidar (light detection and ranging) technology in environmental research. This collaboration eventually led me to the Department of Spatial Sciences where my current supervisor, Petra Šímová, kindly took me in. There, I expanded my research scope, moving beyond traditional field surveys to incorporate remote sensing data for more efficient and precise habitat assessments, leading us to explore other human-influenced habitats, such as spoil heaps from coal mining. Multiple studies have shown that combining forest restoration with areas left to spontaneous succession is a strategy beneficial for supporting species richness in restored sites (e.g., Šálek 2012; Vojar et al. 2016). However, these studies estimated habitat characteristics primarily through field data collection. Although field surveys can provide valuable information, they are labor-intensive and offer limited, subjective estimates. Therefore, we aimed to identify vegetation habitat characteristics that can be easily derived from remote sensing data, offering an efficient and accurate alternative to traditional field surveys.

The first ideas and steps for this research were conceived a long time ago during our year-long stay at the Memorial University of Newfoundland (Canada) in 2014-2015. During this time, Vítek worked in the Marine Geomatics Lab, and I was part of the Shawn J. Leroux Ecosystem Ecology Lab, where I collaborated on research focusing on developing stoichiometric distribution models (Leroux et al. 2017). There is nothing better for conducting research and writing papers than a remote island like Newfoundland. Free from the usual distractions of daily routine, I was able to focus on my dissertation work. However, later on, at the beginning of 2018, in the same month that the first article was finally published, everything changed

rapidly, and diaper changing and sleep deprivation became the daily routine, interrupting research activities for several years.

In summary, my journey from a bird-watching enthusiast to a researcher in ornithology reflects a commitment to unraveling the complexities of how human activities reshape ecosystems and affect wildlife. This work is driven by the belief that a deeper understanding of these dynamics can lead to more informed and impactful conservation efforts, ensuring that animals and their habitats continue to thrive in a rapidly changing world.

Objectives of the Thesis

The main aim of this thesis is to increase our understanding of bird populations in human-altered environments by investigating how environmental conditions affect bird diversity and abundance. This research is based on three studies, each of which contributes unique insights to the fields of bird ecology and biodiversity conservation. The common goal of these studies is to better comprehend the diversity and distributions of birds in human-altered landscapes through evaluating habitat preferences. An additional objective of this dissertation is to provide practical guidelines for urban planning and habitat restoration to support bird conservation and management in various human-altered environments.

Below, an overview of the three studies and their contributions is provided:

The first study focuses on assessing urban habitat preferences on the example of the house sparrow (*Passer domesticus*) and investigates how urbanization impacts their populations. By comparing old and new housing areas, the study identifies critical factors that influence house sparrow abundances. The goal is to provide recommendations for urban planning to support house sparrow populations in new housing developments.

The second study focuses on bird species richness and rarity on a site restored after coal mining. It examines differences in habitat heterogeneity with respect to various restoration approaches (agricultural, forest, or spontaneous succession) and their effects on avian communities. This study employs habitat heterogeneity metrics—such as vegetation structure and senescence—derived from airborne

lidar and hyperspectral data to determine the most effective restoration strategies for promoting bird biodiversity in these restored areas.

Following the insights from the second study, the third study investigates the influence of habitat heterogeneity on bird species richness at a restored site. In addition to the site itself, however, this study also examines its surroundings and focuses on the richness of several bird guilds with diverse nesting, foraging, and feeding behavior. This study examines variations in habitat characteristics similar to those in the second study, but also incorporates terrain characteristics.

Thesis structure

The thesis is a monograph organized into three parts and six chapters. **Part I** includes a preface and a theoretical background, offering a foundational introduction to the thesis and contextualizing the research. **Part II** presents the actual research and consists of three chapters, which are conceived as independent studies, which collectively contribute to a comprehensive understanding of the role of environmental factors in urban and post-mining environments for bird species. **Part III** explores the links among individual studies and their contributions to the overall findings. The studies are listed in the following order:

Study 1 – What makes new housing development unsuitable for house sparrows (*Passer domesticus*)?

Study 2 – The role of the vegetation structure, primary productivity, and senescence derived from airborne LiDAR and hyperspectral data for birds diversity and rarity on a restored site

Study 3 – Habitat heterogeneity derived from lidar and hyperspectral data in a restored site and its surroundings: Implications for bird guilds and restoration management

Chapter II – Theoretical background

The importance of birds for humans

Birds are conspicuous in many habitats, occur worldwide, are ecologically diverse, and are better known than other vertebrate groups. Birds devour pests, pollinate flowers, disperse seeds, scavenge carrion, cycle nutrients, and modify the environment in ways that benefit other species. The ecological significance of birds is well recognized, and the study of their roles within ecosystems has seen substantial growth in recent decades. Research into the functions of bird species and communities, particularly in relation to the direct ecosystem services they provide, has expanded dramatically, reflecting their crucial contributions to biodiversity and ecosystem health.

From the perspective of ecosystem services, birds provide a range of valuable contributions, including provisioning, cultural, regulating, and supporting services (Whelan et al. 2008). Provisioning services are provided by both domesticated (e.g., poultry) and non-domesticated species. Birds have long been important components of human diets and sport (Moss & Bowers 2007). Additionally, bird feathers are used for bedding, insulation, and ornamentation (Green & Elmberg 2014). Birdwatching, a popular recreational activity worldwide, provides direct economic benefits and supports numerous citizen science programs involving bird enthusiasts (Greenwood 2007; Kronenberg 2014; Ma et al. 2013; Sekercioglu 2002).

Birds also contribute significantly to regulating and supporting ecosystem functions through their foraging behaviors. (Whelan et al. 2008). With over 10,000 bird species on earth, birds consume a wide variety of resources in terrestrial, aquatic, and aerial environments. Some consumed resources may be pests of agricultural crops or forests. In other cases, bird resource consumption facilitates pollination or seed dispersal, promoting successful plant reproduction in thousands of plant species. For economically or culturally significant plants, these services benefit humans, who also benefit indirectly from forests and other plants. Through these services, birds have a large, global, but rarely quantified impact on ecosystems (Whelan et al. 2015). Moreover, birds' presence can positively affect human health and well-being, as studies have shown that viewing nature can

decrease recovery time after surgeries; improve blood pressure, cholesterol levels, and outlook on life; reduce stress and mental fatigue; and improve concentration (Bjerke & Ostdahl 2004; Maller et al. 2006). This benefit can be especially important in urban areas where contact with nature is limited.

Altered landscapes

Humans have significantly influenced terrestrial ecosystems for millennia, transforming much of the Earth's surface into anthropogenic land uses (Williams et al. 2020). Mining spoil heaps and urban areas represent significant manifestations of such modified landscapes, showcasing the profound impact of human activities on the environment. These types of landscapes show significant changes in habitat structure and biodiversity. Both these landscapes often show fragmented habitats and altered species composition due to urbanization or mining activities. In addition, management practices such as green space management and ecological restoration efforts further shape these human-altered landscapes. Understanding the ecological conditions and their impact on species within post-mining sites and urban areas is essential for designing effective conservation and management strategies.

Impact of urbanization on birdlife

Urbanization is recognized as an important driver of species decline. Every time we cut down trees, drain marshes, and build houses in their place, we risk harming biodiversity. Urban development is increasing globally, and the expansion of urban areas is among the fastest-growing changes in land use (Gao & O'Neil 2020). This is partly due to human population growth, but also arises from socio-economic factors that result in people moving from rural to urban areas, a greater proportion of single-person households, and elevated demand for low-density housing (Liu et al. 2003).

There are three main reasons why increased urban development negatively affects biodiversity. First, urbanization is most likely to occur in regions that contain large numbers of people; this results in conservation conflicts because, at broad spatial scales, human population density is positively correlated with species richness (Evans et al. 2007; Luck 2007). Second, the land selected for housing development

is often more ecologically valuable than other areas (Bartlett et al. 2000; Gonzalez-Abraham et al. 2007; Radeloff et al. 2010). Third, highly developed urban areas support fewer native species than the rural habitats they replace. Indeed, many species do not occur in urban areas despite being present in nearby rural habitats (Tratalos et al. 2007; Grimm et al. 2008).

Urban birds represent a unique area of study within the field of ornithology. Research on urban birds involves examining factors such as habitat preferences (Choudhary et al. 2019), foraging strategies (Bernat-Ponce et al. 2018), and responses to anthropogenic disturbance (Vincze et al. 2016). Urbanization affects bird communities, leading to changes in species composition, abundance, and distribution patterns. By studying urban birds, we are gaining insights into the mechanisms that cause these changes, including habitat fragmentation, pollution, and the availability of food resources. In addition, urban areas provide valuable opportunities to investigate topics such as bird-human interactions, including the effects of urbanization on bird behavior and physiology, and the potential benefits and challenges of bird coexistence in human-dominated landscapes (e.g. Meillère et al. 2017; Bernat-Ponce et al. 2018).

Of all wild birds, none is more closely associated with humans than the house sparrow (*Passer domesticus*), which is one of the most ubiquitous passerines globally (e.g., Berigan 2020). Just a few decades ago, it would have been unimaginable for the house sparrow to be a topic of discussion at an international ornithological or environmental conference. However, the house sparrow, particularly the urban house sparrow, has since become a focus of study for several national and regional ornithological organizations across Europe (De Laet & Summers-Smith 2007). This shift in focus has been driven by the notable and widespread decline in house sparrow populations, which has raised concerns about broader environmental and ecological changes (Robinson et al. 2005; De Laet & Summers-Smith 2007; Shaw et al. 2008; Singh et al. 2013; Berigan et al. 2020).

Housing development impacts biodiversity in a number of ways, including altered disturbance regimes, light and noise conditions, habitat distributions, and species composition (Turner et al. 2004; Alberti 2005; Miller 2005). In addition, the climate of urban areas differs from that in nearby rural environments due to the urban heat island phenomenon (Wang et al. 2023). Therefore, urban areas have longer growing seasons than nearby rural habitats. Such changes in urban habitats have forced animals and plants to either adapt or disappear (Hunter 2007).

However, the urban environment does not affect all species equally. While many bird species are losing their habitat due to urbanization and their populations are

declining, other bird species are benefiting from the expansion of urban areas. Numerous species have adapted to the proximity of humans (Møller 2009; Evans et al. 2011). Interestingly enough, population densities of species that have lived for a long time in urban environments, such as feral pigeons (*Columba livia domestica*), house sparrows (*Passer domesticus*), and blackbirds (*Turdus merula*), have become considerably higher than their populations in nearby rural habitats (Luniak 2004).

In general, habitat conversion has a negative effect on rare and specialist species, while it favors generalists and behaviorally flexible species (Møller 2009). Species vary widely in their environmental tolerances, and generalists appear less vulnerable to habitat deterioration and loss (Owens & Bennett 2000; Shultz et al. 2005), including urban development (Bonier et al. 2007; Kark et al. 2007). Behavioral flexibility may also help species tolerate environmental change. Measurements of flexibility, such as the acquisition of new foraging techniques, are correlated with relative brain size (Healy & Rowe 2007), which has also been shown to be associated with population trends (Shultz et al. 2005). Therefore, urbanization may also promote behaviorally flexible species with relatively larger brains.

Moreover, urban environments offer unique challenges and opportunities that further influence species distribution. Urban areas often provide abundant anthropogenic food resources (Robb et al. 2008) and supplementary avian food, primarily consisting of seeds or other plant material (Davies et al. 2009). As a result, species capable of exploiting these resources may become more prevalent in urban areas compared to those with alternative diets (Fuller et al. 2008; Evans et al. 2011). In contrast, insectivorous species tend to be relatively scarce in urban settings (Chace & Walsh 2006; Kark et al. 2007). However, the presence of supplementary food is just one factor influencing bird populations. For example, urban areas may also pose higher predation risks due to changes in habitat types (Riley et al. 2005; Hamer & McDonnell 2008) and increased densities of predators such as domestic cats (*Felis catus*) and nest-predating corvids (Sims et al. 2008; Evans et al. 2009).

Mining, restoration, and their effect on (bird) diversity

Mining is a major global industry with the potential to significantly enhance a country's economy, but the environmental impacts of mining are significant. It is one of the most destructive human activities considerably altering large areas worldwide (Slonecker & Benger 2001). Establishing mining sites requires an

enormous amount of construction, which often causes deforestation and loss of wildlife habitats and biodiversity. While much of the world's mining activity occurs in resource-rich countries like Russia, China, and Australia, European countries such as Germany, Ukraine, and Czechia also have a significant history of mining and are struggling with the ecological impacts of both current and past mining operations (Krümmelbein et al. 2012; Maus et al. 2022).

Post-mining sites, such as spoil heaps, strip mines, and quarries, are classic examples of heavily disturbed ecosystems where extensive anthropogenic land modifications have severely altered the natural functioning of the landscapes. Minimization of the negative effects of mining is typically ensured by ecological restoration, i.e., a process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Clewell & Aronson 2013, Martins et al. 2020). Unlike urban areas, restored post-mining sites often aim to mimic natural habitats, which can support a wide range of species. The goal is to create self-sustaining ecosystems that, over time, can support the same or even greater biodiversity than before mining. This is driven by regulatory requirements and increasing environmental awareness but also by the recognition of the ecological and social benefits that restored habitats can provide (Šálek 2012; Wortley et al. 2013).

In European contexts, restoration efforts often involve technical reclamation practices (Hodačová & Prach 2003). This process typically includes (i) surface leveling, (ii) soil amendment, and/or (iii) surface treatment, followed by (iv) revegetation, i.e. over-seeding or afforestation (Štýs & Braniš 1999; Holl 2002; Hendrychová 2008). Surface leveling involves smoothing the terrain to create a stable and uniform surface. It helps to prevent erosion and prepares the site for further reclamation activities. The goal is to stabilize the soil and make it suitable for vegetation establishment. Soil amendments, which involve adding organic matter like compost or manure, and other conditioners, enhance soil fertility, balance pH, and improve soil structure, all of which are essential for supporting healthy plant growth. Surface treatments involve applying topsoil to create a suitable medium for plant establishment. Often, the soil is enriched with essential nutrients and organic matter to enhance its quality. Over-seeding involves sowing a mixture of grass and herbaceous plant seeds to quickly establish ground cover, which helps prevent erosion and creates initial habitat conditions, while afforestation focuses on planting trees to restore forest cover based on the restoration goals and site conditions (see review by Navarro-Ramos et al. 2022).

Importantly, technical reclamation often leads to habitat impoverishment and reduces the natural potential of restored sites for biodiversity and conservation.

Technical reclamation typically begins once the heaped material has stabilized, usually several years after deposition. This timing often coincides with the point at which spontaneous succession has advanced to a stage where perennials begin to dominate and establish a more cohesive vegetation cover, generally around the 15th year of succession (Hodačová & Prach 2003). Consequently, restored sites are sometimes subjected to technical reclamation despite their potential to recover naturally, which can lead to the replacement of unique and diverse plant communities with species-poor grass mixtures or tree plantations, ultimately proving counterproductive for biodiversity (Prach et al. 2013). However, in many cases, technical reclamation is not necessary for effective ecosystem restoration. Post-mining sites can be left to undergo natural succession without intervention, including the preservation of the original terrain character created by the heaping process, which typically forms an undulating landscape. This results in the development of more diverse plant communities and better habitats for rare species compared to technically reclaimed sites (Tropek et al. 2012; Hendrychová et al. 2012; Šálek 2012; Řehounková et al. 2020). Therefore, leaving disturbed sites unreclaimed can be a cost-effective management strategy (Řehounková et al. 2018) that is actually beneficial to the environment.

Historically, animals, including birds, have been overlooked in restoration activities (but see Bejček & Šťastný 1984). However, in recent decades, birds have increasingly become a focal point in restoration ecology research (Ortega-Álvarez & Lindig-Cisneros 2012). They play a crucial role in the colonization of restored habitats on spoil heaps due to their high dispersal ability, often being among the first groups to populate these areas (Martins et al. 2020). Nevertheless, not all bird species are equally attracted to post-mining sites. The success of the colonization of such sites by birds depends on adopted restoration approaches that affect habitat structure (Korejs et al. 2024), food availability (Day et al. 2017), and predation risks (Novák & Hendrychová 2021). Studying birds in restored habitats provides valuable insights into the effectiveness of various restoration strategies, such as spontaneous succession versus active reforestation (Šálek 2012; Korejs et al. 2024). For instance, it has been shown that sites left to spontaneous succession can develop valuable communities of specialists that are scarce in the surrounding landscape, while technically reclaimed sites result in impoverished communities, usually with narrow spectra of common species (Šálek 2012). Conversely, species that nest in trees may prefer forest-type reclamations. Additionally, restored areas provide opportunities to study the role of birds in ecosystem recovery processes, such as seed dispersal (Sampaio et al. 2021). Enhancing our understanding of birds

in the restoration process can contribute to the development of innovative approaches that address all aspects of ecosystem restoration.

Role and measuring of vegetation structure

Birds are highly dependent on the structure of vegetation, which plays a critical role in their foraging, nesting, and sheltering behaviors. Heterogeneity in vegetation structure is an important predictor of both bird species richness and habitat quality for individual species, at a range of spatial scales (Hinsley et al. 1998, Chamberlain & Gregory 1999, Benton et al. 2003, Wilson et al. 2005). Birds' ability to navigate various vertical layers of vegetation, such as the upper canopy, mid-layers, and understory, makes them sensitive indicators of changes in vegetation structure. Vertical complexity and horizontal distribution of vegetation directly influence bird species diversity and abundance. Vegetation structure may impede the movement of foraging birds both physically (Brodmann et al. 1997) and behaviorally (Desrochers & Hannon 1997) and may influence foraging efficiency through its effects on the detectability and accessibility of food items (e.g. Moorcroft et al. 2002, Whittingham & Markland 2002). For instance, the abundance of wading birds in grasslands is often correlated with vegetation height, which affects movement ease and soil penetration during feeding, and thus prey intake rate (Milsom et al. 2000). Within specific habitat units, such as forests or agricultural fields, the variety in vegetation can affect bird and invertebrate distributions. For example, while dense vegetation might support certain invertebrates, birds may prefer adjacent sparser areas where movement and access are easier (Morris et al. 2002; Perkins et al. 2002). Vegetation structure also influences predation risk and breeding success, balancing concealment with visibility. This trade-off varies among predators and is influenced by the prey species' antipredator responses (Götmark et al. 1995).

Given the importance of vegetation structure, its accurate capture is crucial. The time and labor costs of collecting structural vegetation data manually mean that there is often a trade-off between the level of detail of observation and the size of the area that can be surveyed. As an example that illustrates the contrast between the methods used in the past and the present to collect data on species–

environment relationships , we can name the study by MacArthur & MacArthur (1961). The method they used to measure vegetation structure was extremely laborious and virtually precluded the collection of such environmental data for large areas-they looked through an aluminum tube and counted the numbers of visible leaves.

Although it is still common to estimate vegetation structure from field surveys and although such data can provide insights into habitat heterogeneity and its importance to individual species (Kolar et al. 2021; Poláková et al. 2022; Delheimer et al. 2023), traditional field surveys are temporarily and spatially limited by their labor-intensiveness. In addition, they provide only rough subjective estimates of vegetation cover typically represented by semiquantitative or categorical measures with limited informative value (Vojar et al. 2016; Kolář et al. 2017; Bellamy et al. 2022).

Remote sensing methods, on the other hand, provide cost-effective and less labor-intensive alternative for collecting habitat data (Skidmore et al. 2021). It is relatively common to use data from passive remote sensing approaches, which involve capturing reflected sunlight to gather information about the Earth's surface (Lillesand et al. 2015). The use of orthophotomaps is a relatively straightforward and efficient method for identifying and mapping vegetation over larger areas. Orthophotomaps are high-resolution aerial images, typically captured using RGB cameras, which have been geometrically corrected to ensure a uniform scale (DeWitt & Wolf 2000). By interpreting these images, scientists can classify different types of vegetation and assess their spatial distribution. This process often involves manual identification and vectorization in GIS (geographic information systems), where scientists digitize vegetation types and boundaries between them directly from the images. Although vectorization allows the creation of detailed maps that can highlight specific habitat features and changes over time, the process is still extremely labor-intensive. The advantage of this method over field surveys lies in its ability to cover larger areas and to provide insights into inaccessible places, such as private gardens and yards.

For a more advanced analysis, multispectral or hyperspectral sensors can be employed to monitor vegetation health and horizontal distribution in even greater detail (Lillesand et al. 2015). These sensors capture data across different wavelengths, enabling the use of spectral indices such as the Normalized Difference Vegetation Index (NDVI; Tucker 1979) and the Plant Senescence Reflectance Index (PSRI; Merzlyak et al. 1999). NDVI is commonly used to assess the greenness and overall health of vegetation, while PSRI is effective for detecting

signs of senescence or plant stress. By utilizing these spectral indices, vegetation cover and its heterogeneity over large areas can be quantified, offering a comprehensive view that is not achievable with ground-based surveys alone. However, a major disadvantage of passive remote sensing is that it only captures horizontal heterogeneity and does not provide information about the vertical structure below the canopy, which is critical for understanding the full complexity of vegetation architecture.

To address this limitation, active remote sensing technologies such as laser altimetry, or Light Detection and Ranging (lidar), offer a more comprehensive approach to collecting vegetation structure information (Vierling et al. 2008; Bergen et al. 2009). Airborne laser scanning, i.e., a lidar sensor on board an airplane, has now become the main method for collecting accurate terrain and vegetation structure over large areas (e.g. Melin et al. 2017; Wehr & Lohr 1999). Laser altimetry is an active remote sensing method that uses laser beams to measure distances between the sensor and a target surface and thus determine the positions of objects in three-dimensional space. A key advantage of airborne lidar over methods such as digital aerial photogrammetry is represented by the fact that laser pulses can pass through gaps in the canopy and register multiple returns, providing detailed information from different depths within the vegetation and, at the same time, capturing the terrain under vegetation canopy (Wehr & Lohr 1999). Among remote sensing methods, lidar, particularly airborne laser scanning, offers the ability to record variation in vegetation height at an ideal spatial resolution for parameterizing bird–habitat models. The disadvantage may lie in the need for some technical knowledge to process lidar data (Assmann et al. 2022).

When combined, hyperspectral and lidar data provide a powerful toolset for ecological studies. Hyperspectral sensors capture detailed information about the spectral properties of vegetation, revealing insights into plant health and stress levels, while lidar provides precise measurements of vertical vegetation structure. This complementary use of passive and active remote sensing technologies enables a more complete understanding of both the horizontal and vertical dimensions of vegetation, offering a holistic view invaluable to ecological research.

Chapter III– Study 1

Title: What makes new housing development unsuitable for house sparrows (*Passer domesticus*)?

Authors:

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Author's contribution:

Conceptualization, Data gathering, Data Curation, Methodology, Writing - original draft, Writing - review and editing

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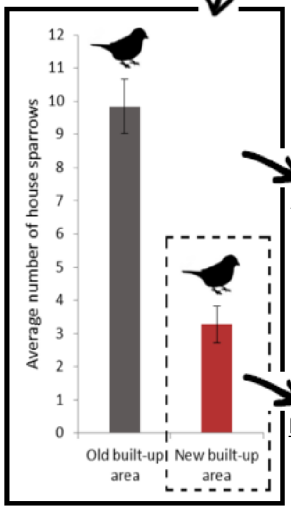
Cited:

23 times cited on WOS (October 2024)

Graphical Abstract:

60 urban settlements
4 ha square plots
62 sites in old built-up areas
and 62 sites in new built-up areas



Habitat composition and occurrences of potential competitors

Predictor	mean (range) for old built-up areas	mean (range) for new built-up areas
Greenery cover	27% (10% - 40%)	12% (0% - 20%)
Collared dove*	— (0 - 1)	— (0 - 1)
Backyard poultry*	— (0 - 1)	— (0 - 1)
Cropland and grassland	35% (0% - 70%)	50% (20% - 85%)
Built-up area	43% (30% - 60%)	40% (30% - 60%)
Tree sparrow*	— (0 - 1)	— (0 - 1)

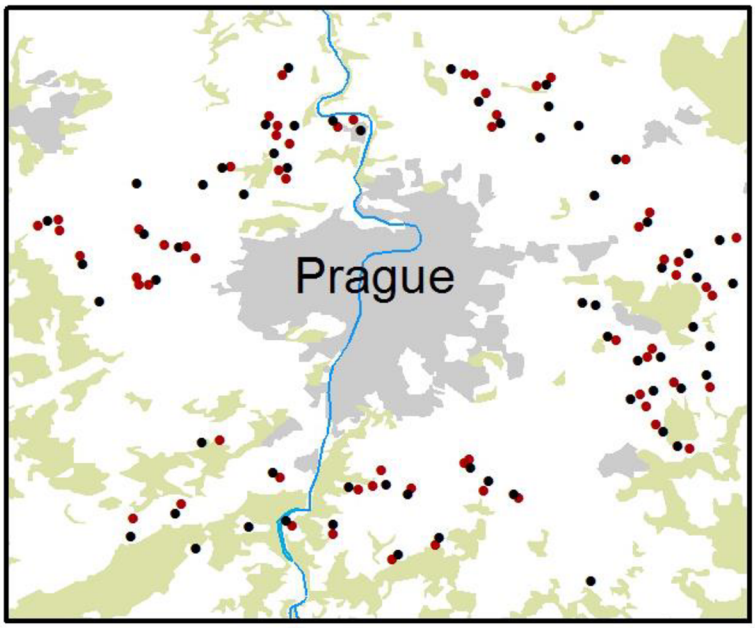
* presence/absence variables

House sparrows on sites in both old and new build-up areas

House sparrows showed strong preferences for old built-up areas compared with new built-up areas. Presence of collared doves and backyard poultry were the most important predictors positively influencing house sparrow numbers. There was also a positive effect of increasing proportion of greenery cover. Total proportion of built-up area, presence of tree sparrows, as well as proportion of cropland and grassland in the surroundings remained without significant effect on numbers of house sparrow males.

House sparrow on sites in new build-up areas

The only variable significantly influencing house sparrow numbers in new built-up areas was greenery cover. Distance from older built-up area and age of newly built-up area were the variables specific only for newly built-up areas. However, neither of them significantly



• Old build-up area • New build-up area

Abstract

As a species closely associated with people and urban areas, the house sparrow (*Passer domesticus*) was expected to prosper with increased urbanization. Over the past few decades, however, house sparrow populations have decreased in many towns and cities around the world. The most commonly mentioned reasons for these decreases are lack of food, especially invertebrates, and fewer nesting sites and shelters. Given the need to evaluate the role of newly built homes and their effect on sparrow habitat, our overall goal was to evaluate if new housing areas are inhabited with a lower density of house sparrows than old housing areas and, if so, to identify factors responsible for the differences. We carried out observations in 60 small settlements in the greater municipal area of Prague, Czech Republic. Our results indicate house sparrows' high preference for old parts of settlements and unsuitability of newly built-up areas. Backyard poultry's presence and sufficient green space were both important factors related to house sparrow abundances. Specifically, house sparrow abundance was highest in sites with 20% to 30% greenery cover (trees and shrubs) and they exploited sites that had backyard poultry. We found no effect of other granivorous birds acting as competitors. Instead, house sparrow abundance was higher where another granivorous species were present. As a measure to sustain greater biodiversity in modern housing development, we suggest increasing trees and shrubs cover in newly built-up areas to a minimum of 20%.

Keywords:

urban birds, urban ecosystems, backyard poultry, residential areas, greenery cover

Introduction

Urban areas are growing rapidly throughout the world, and this trend is expected to continue as urban areas absorb most of the global population growth in the future (United Nations 2011; Kourtit et al. 2014). Numerous species have adapted to the proximity of humans (Evans et al. 2011; Møller 2009) and the biodiversity of urban areas has gained more attention with continuous urbanization (Pickett et al. 2011). Further investigation of species' responses to urban environments is important for understanding synurbic populations and their implications for urban

biodiversity and management (Francis & Chadwick 2012). One useful group for understanding urban biodiversity are birds, which are the dominant group of vertebrates in urban areas (Campbell 2007). Amongst birds, none is more closely associated with man worldwide than the house sparrow (*Passer domesticus*) (Peach et al. 2008).

In 1963, J.D. Summers-Smith predicted that house sparrow populations would increase with man's global dominance and the increasing amount of built-up land, which is the preferred habitat for the bird. However, four decades later, Summers-Smith was the first to admit how wrong he had been (De Laet & Summers-Smith 2007). In the last decade numerous studies have reported evidence of a rapid decrease in house sparrow populations in many European towns and cities (Shaw et al. 2008). For instance, in urban–suburban Britain, with solid long-term observations, the decline appears to have begun in the mid-1980s and continued throughout the 1990s (Robinson et al. 2005; Summers-Smith 2003). A similar trend has been reported in India (Singh et al. 2013) and over parts of the bird's non-native range in North America (Erskine 2006) and Australia (Olsen et al. 2003). Although populations are declining in many places, there also are regions with stable or increasing numbers of house sparrows (Shaw et al. 2008).

The first record of house sparrow decline comes from the beginning of the 20th century. At that time, automobiles had replaced horse-drawn transport and caused a decrease in seed, a food resource from horse feeding and indigestible remains (Summers-Smith 2005). Lack of food is still one of the causes of the birds' decline most often cited (Murgui & Macias 2010; Peach et al. 2008; Singh et al. 2013). The main reason, however, is not a lack of seeds (De Coster et al. 2015) but rather a decrease in invertebrate abundance (Peach et al. 2008). Although, adult house sparrows have mostly a plant diet (Cramp & Simmons 1994), invertebrates comprise an important part of their diet during the breeding season and are necessary for feeding nestlings. Shortage of these invertebrates may cause a reduction in clutch size (Peach et al. 2014) and higher chick mortality (Peach et al. 2008; Seress et al. 2012). For instance, Peach et al. (2015) found large positive impact on the abundance of recently fledged birds, but only a small positive impact, limited mainly to small colonies, on the overall abundance of territorial males. Lack of invertebrates may be linked with the presence of fewer vegetated areas in modern municipalities. For example, Turrini & Knop (2015) found a link between arthropod diversity and abundance and sufficiency of vegetated space in urban areas. Availability of invertebrates also could be negatively affected by the use of pesticides or planting of exotic species which are typical for modern gardening. House sparrows collect invertebrates from deciduous woody

vegetation, trees, and grassland rather than from evergreen or ornamental shrubs (Vincent 2005).

House sparrows are very flexible in using a variety of structures as nesting sites (Summers-Smith 2009). However, modern buildings may have changed the availability of nesting sites. New housing technologies using different materials offer fewer holes and cracks (Shaw et al. 2008; Singh et al. 2013), whereas old crumbling buildings with holes under roofs, cracks in siding, and unkempt surroundings offer more shelters and nesting sites. In addition, a shortage of potential nesting sites and shelters increases predation risk. Domestic cats (*Felis catus*) and sparrowhawks (*Accipiter nisus*) are the most cited predators of house sparrows in urban areas (De Coster et al. 2015; Summers-Smith 2003). For example, domestic cats have been estimated to kill yearly as many as 27 million birds in the UK between 1 April and 31 August (Woods et al. 2003).

Much has been written about the causes of house sparrow decline and many of the aforementioned studies refer to the coincidence of several factors that are mostly associated with fewer nesting sites, shelters, and invertebrates. Furthermore, Shaw et al. (2008) had suggested that the house sparrow population in many cities is more abundant in areas with low socioeconomic status as compared to more affluent areas. Moreover, Wotton et al. (2002) revealed that houses built before 1919 are important as a source of nesting sites. Thus, it is possible that changes in all of these important factors might be explained by complex changes in housing development even on a smaller scale within particular human settlements. However, there have been no studies to date that have included the aging process of new housing areas as a factor which may influence their suitability for house sparrows. Measuring the abundance of house sparrows in newly built-up areas of different ages can point to possible trends in house sparrow populations in the future.

Given the need to evaluate the role of newly built homes and their effect on sparrow habitat, our overall goal was to evaluate if new housing areas are inhabited with a lower density of house sparrows than old housing areas and, if so, to identify factors responsible for the differences. To address this goal we sought to answer the following questions: 1) Is there any difference in house sparrow numbers between old and new housing areas? 2) Do total amount of trees and shrubs (hereinafter termed greenery cover), extent of built-up area, presence of backyard poultry and potential avian competitors affect house sparrow numbers in residential housing areas? 3) Are newly built-up areas more suitable for house sparrows as they get older or/and in relation to distance to older built-up areas?

Methods

Research area

The Czech Republic provides a suitable model country with a clear separation between old and modern housing developments due to rapid change from a centrally planned to a market economy with significant economic growth after the Velvet Revolution in 1989. The political and economic changes initiated the start of suburban growth (Ouředníček 2007). Whereas old parts of settlements had been established prior to 1940 and their area almost has not changed, a major suburbanization process began after 1989 and new parts of settlements have grown up rapidly. These specific conditions of urban development allow us to compare modern housing with older-style housing on a local scale. With the improved economic situation and mobility, many people have moved from cities to neighboring villages. Thus, housing development has gone through a dramatic change as new residential areas have grown up around original settlements to occupy agricultural fields and grasslands. Original built-up areas also have undergone transformations. Renovation of old buildings is slower than constructing new buildings on a green field.

Study sites

This study was carried out at 124 sites in 60 small, moderately developed urban settlements (Francis & Chadwick 2012) located within 25 km from the center of Prague, the capital city of the Czech Republic (Fig. 1). The entire area has undergone significant urban–suburban housing development. New parts of settlements (hereinafter termed new built-up areas) are characterized as uniform housing segments built up after 1990 and connected with any older built-up area as a possible source of birds. Old parts of settlements (hereinafter termed old built-up areas) are uniform housing segments situated in original parts of settlements that have been built up continually before World War II. Sample plots were 4 ha squares (hereafter referred to as sites) where birds were counted. The sites were located in residential areas with a dense network of roads sufficient for easy access to all parts (Fig. 2).

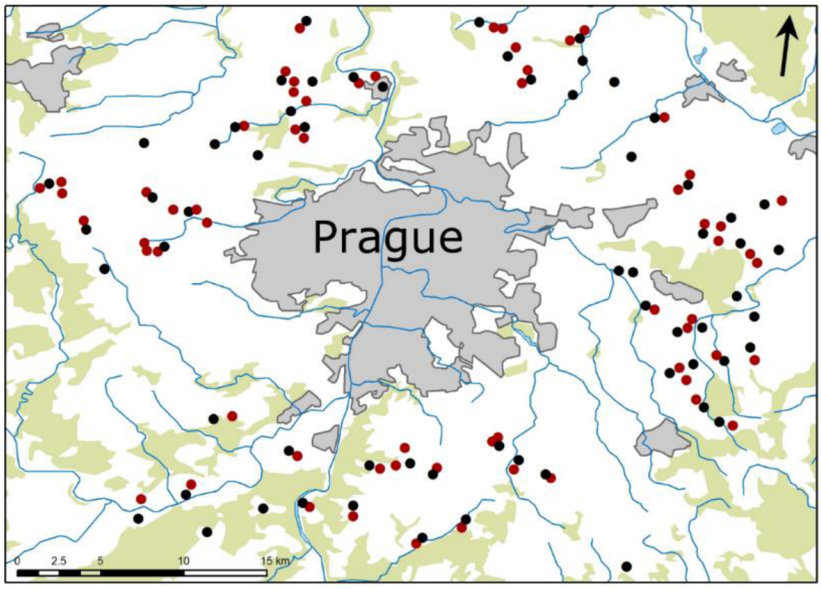


Fig. 1. Locations of stud sites around Prague: new built-up areas (red) and old built-up areas (black); Krovak Oblique Conformal Conic Projection.

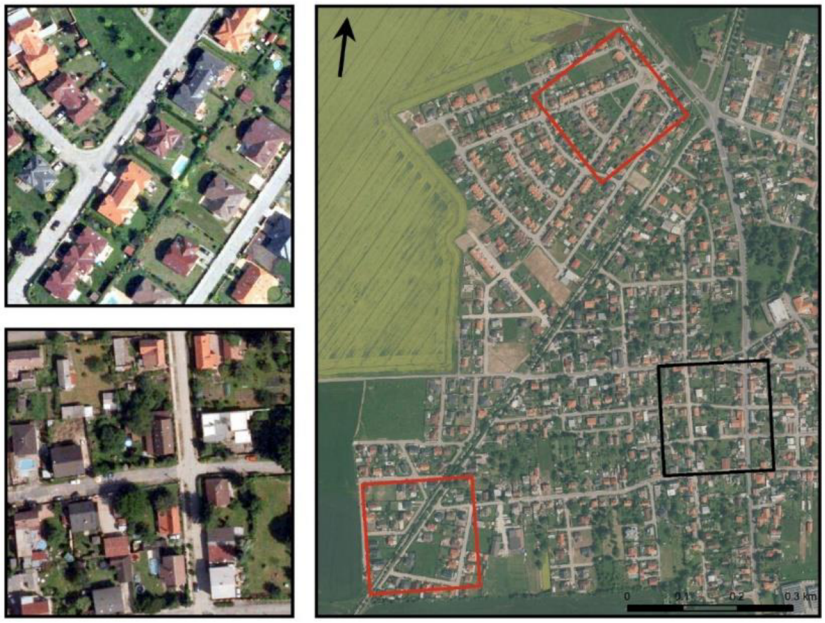


Fig. 2. Example of study sites in settlement: new built-up areas (red) and old built-up area (black). Frames on the left side shows details of new built-up area (on the top) and old built-up area (on the bottom); Krovak Oblique Conformal Conic Projection.

In every settlement at least one site was situated in an older built-up area. In addition, zero to three sites were selected in newly built-up areas according to their availability in the settlement. The sites were at least 300 m apart to avoid double counting of birds. Consequently, we defined one site in newly built-up areas in 28

settlements, two in 11 settlements, and three in 4 settlements. We were unable to define coherent newly built-up areas in 17 of the settlements.

Study variables

All variables were quantified for 4 ha squares, except of proportion of cropland and grassland. In addition to abundance of house sparrows, we recorded presence/absence of collared dove (*Streptopelia decaocto*) and tree sparrow (*Passer montanus*) as possible competitors having similar diet and habitat requirements (Summers-Smith 2003). As a possible source of food, we also recorded presence/absence of backyard poultry within the sites. Presence of poultry was recorded during morning surveys, and then one more visit of each site was conducted in afternoon hours when poultry are more active and easily detectable. In addition to competing species and backyard poultry, the following variables were roughly estimated by one person with precision of ±5% (greenery cover and built-up area) and ±2.5% (cropland and grassland) using orthophoto images from 2012 and then validated against the current state as recorded during the site visits (see Seress et al. 2014): 1) proportion of greenery cover (trees and shrubs); 2) proportion of built-up area; and, 3) proportion of cropland and grassland (cropland or grassland within 500 m radius from center of the site). To verify the adopted classification approach, we created polygons of greenery cover, built-up area, and area of cropland and grassland from orthophotos for 10 randomly selected sites (5 in new and 5 in old built-up areas) and calculated areas of the polygons. Comparisons of rough estimates and time-consuming exact measures revealed strong correlation (all $r \geq 0.75$; $P \leq 0.01$), thus suggesting the rough estimates to be sufficient substitutes for exact estimates.

We estimated all the aforementioned variables for both newly and older built-up areas. Furthermore, for sites in newly built-up areas we measured distances to any nearest older built-up area regardless of whether it was designated as a sample site or not and estimated the age of housing. Age of housing was classified under three categories based on aerial orthophoto maps from three periods (2003, 2006 and 2012; i.e. 9 years old, 6 years old, and newly established housing, respectively). This method is more representative than administrative records because birds can inhabit buildings before they are officially registered. Distance between new and nearest older built-up area was measured in meters. All operations with geodata were processed using ArcGIS 10.2 (ESRI, CA, USA).

Statistical analyses

Before analysis, we checked collinearity among log-transformed continuous variables (greenery cover, built-up area, cropland and grassland for old build-up areas and distance from nearest older built-up area for newly built-up area) to avoid artificially inflating the standard error of parameter estimates. Neither pair of continuous predictors had Pearson's $r > 0.6$ which we adopted as a criterion for strong correlation so all predictors entered the models. The differences in habitat variables between old and new built-up areas we compared using generalized mixed-effect model (GLMM) with binary (0 vs 1) response (old or new built-up area) and a settlement ID as a random factor. In the complex analysis of factors influencing abundance of House Sparrow males in plots, we ran a Poisson generalized mixed-effect models (GLMM) with abundances of males as explained variable and, again, the settlement ID as a random factor (McCullagh & Nelder 1989). As house sparrows may occur in flocks, we calculated the dispersion parameter to check for overdispersion (see Ver Hoef & Boveng 2007). As the dispersion parameter varied between 0.7 (model for new built-up areas) and 1.4 (model for old and new built-up areas), we used a Poisson model with log link function (see Ver Hoef & Boveng 2007). We present significances based on model chi-square with α stated at 0.05 and type 3 testing (i.e. testing an effect while controlled for effects of the remaining ones) (Crawley 2007). The GLMM we fitted using the function (glmer) in package 'lme4' in R 3.1.2. (R Development Core Team, 2014). Overdispersion was checked using the function (overdisp_fun). All results are presented as means ± SE, unless otherwise noted.

Results

Comparison of old and new built-up areas

New and old built-up areas differed significantly in most measured variables (Table 1). In particular, old built-up areas were associated with significantly higher proportion of greenery cover, total built-up area but with lower proportion of surrounding cropland and grasslands. In addition, old built-up areas were accompanied by more frequent occurrences of collared doves and backyard

poultry. However, the differences in presence of tree sparrows between new and old built-up areas was not significant.

House sparrows were recorded at 85.5% of 124 studied sites with 813 individual males. However, house sparrows showed strong preferences for old built-up areas compared with new built-up areas (Fig. 3). Specifically, while house sparrows were present on all of the old built-up areas, only 71% of new built-up areas were occupied (test of proportions: $\chi^2 = 18.78$; $P < 0.0001$). Similarly, in male house sparrow abundance was significantly different between the two types of built-up sites (9.8 ± 0.81 vs 3.3 ± 0.56 for old vs new built-up areas, respectively; Wilcoxon test: $W = 506.5$, $P < 0.0001$).

Table 1. Comparison of predictors between old and new parts of a settlement (expressed as a binary response in the model). Positive estimates indicate higher values in new parts and negative estimates mean higher values in old parts.

Predictor	mean (range) for old built-up areas	mean (range) for new built-up areas	sites with presence in old/new built-up areas	Estimate	se	df	χ^2	P
Greenery cover	**27% (10%-40%)**	**12% (0%-20%)**	**—**	**-0.362**	**0.0387**	**1,3**	**67.012**	**<0.0001**
Collared dove*	**— (0 - 1)**	**— (0 - 1)**	**56/22**	**-0.549**	**0.0720**	**1,3**	**48.221**	**<0.0001**
Backyard poultry*	**— (0 - 1)**	**— (0 - 1)**	**35/8**	**-0.435**	**0.0766**	**1,3**	**29.120**	**<0.0001**
Cropland and grassland	**35% (0%-70%)**	**50% (20%-85%)**	**—**	**0.18**	**0.0393**	**1,3**	**18.774**	**<0.0001**
Built-up area	**43% (30%-60%)**	**40% (30%-60%)**	**—**	**-0.032**	**0.0162**	**1,3**	**3.834**	**0.05**
Tree sparrow*	— (0 - 1)	— (0 - 1)	23/31	0.133	0.0815	1,3	2.637	0.104

* presence/absence variables

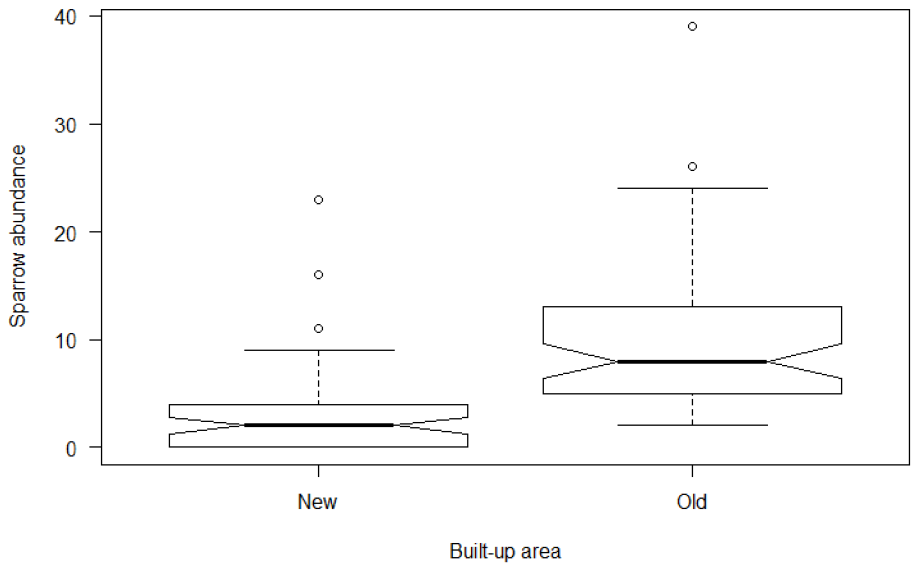


Fig. 3. House sparrow males per 4 ha site in newly and older built-up areas.

Variables explaining house sparrow abundance

Presence of collared doves (Fig. 4) and backyard poultry (Fig. 5) were the most important predictors positively influencing house sparrow numbers (Table 2). There was also a positive effect of increasing proportion of greenery cover. Total proportion of built-up area, presence of tree sparrows, and the proportion of cropland and grassland in the surroundings were unrelated to the number of house sparrow males.

Table 2. Effects of predictors on abundance of house sparrows in both old and new built-up areas; results of full mixed effect model.

Predictor	Estimate	se	df	χ^2	P
Collared dove	**0.798**	**0.1252**	**1,7**	**41.072**	**< 0.0001**
Backyard poultry	**0.537**	**0.1015**	**1,7**	**27.923**	**< 0.0001**
Greenery cover	**1.199**	**0.2754**	**1,7**	**21.665**	**< 0.0001**
Built-up area	-0.230	0.5321	1,7	0.184	0.668
Tree sparrow	-0.140	0.1142	1,7	1.486	0.223
Cropland and grassland	-0.096	0.2163	1,7	0.194	0.659

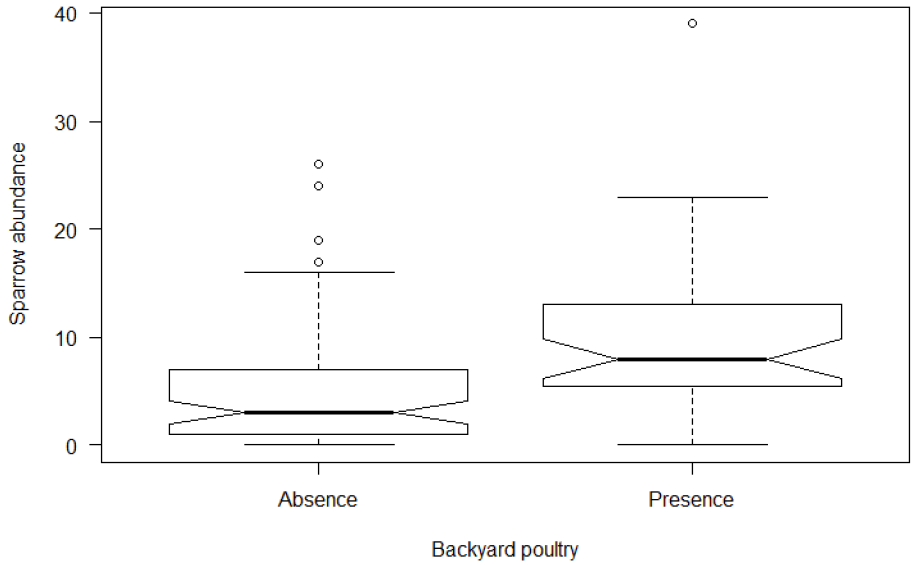


Fig. 4. House sparrow males in sites with/without backyard poultry.

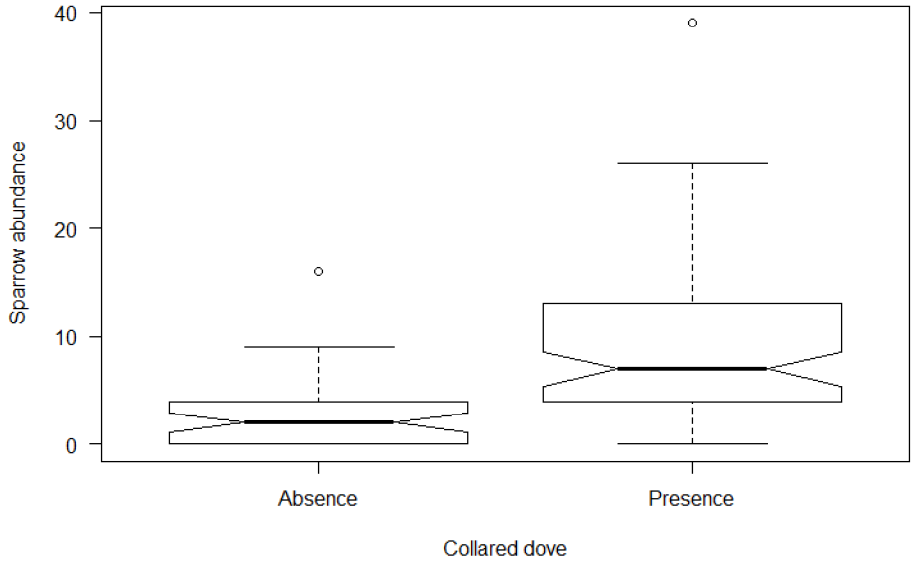


Fig. 5. House sparrow males in sites with/without collared dove.

Newly built-up areas

We recorded 203 House Sparrow males at 62 sites of new built-up areas. The only variable significantly influencing house sparrow numbers in new built-up areas was greenery cover (Table 3). Distance from older built-up area and age of newly built-up area were the variables specific only for newly built-up areas, but neither of them significantly influenced abundance of house sparrow males.

Table 3. Effects of predictors on abundance of house sparrows in newly built-up areas: results of full mixed effect model.

Predictor	Estimate	se	df	χ^2	P
Greenery cover	**1.485**	**0.7477**	**1,6**	**4.527**	**0.033**
Collared dove	0.431	0.2724	1,6	2.433	0.119
Backyard poultry	0.508	0.3577	1,6	1.889	0.169
Age of built-up area	-0.239	0.2106	1,6	1.288	0.256
Distance from older built-up area	0.006	0.1529	1,6	0.002	0.967

Discussion

Our study found a notable difference in the number of house sparrows between old and new built-up areas, despite belonging to one settlement. We found great variability in house sparrow numbers in different parts of villages and towns according to changing urban development. The numbers of house sparrows were higher in sites where backyard poultry was present and was positively correlated with proportion of greenery cover. On the other hand, and similar to Mason (2006), the presence of potential competitors (tree sparrows or collared doves) was not negatively related to house sparrow abundance. In addition to that, we found no effects of proportion of cropland and grassland near new housing areas.

The abundance of house sparrows was most positively influenced by the presence of backyard poultry. The highest number of house sparrows occurred at those sites within which poultry were present. At the same time, presence of backyard poultry was one of the predictors showing a strong bias toward older built-up areas. Presence of backyard poultry can increase the availability of seeds as well as invertebrates which constitute a significant component of house sparrow food

(Cramp & Simmons 1994). Poultry are hosts for a number of invertebrates, and poultry manure also positively affects numbers of invertebrates (Delgado et al. 2012). Consistent with other studies (e.g. Murgui & Macias 2010; Peach et al. 2008; Singh et al. 2013), we suggest that food shortage is one of the main causes of house sparrow decline. Although experimental supplementary feeding had no effect on house sparrow numbers, supplementary feeding of mealworms did enhance their reproductive success (Peach et al. 2015, 2014). Backyard poultry likely provides an important yearlong food resource (Šálek et al. 2015), and presence of backyard poultry could be even critically important in new built-up areas due to a lack of other food sources. However, a general scarcity of variation in backyard poultry in our data for new built-up areas did not allow us to reliably assess this effect.

Similarly, a positive effect was shown by amount of greenery cover. This positive effect is not a surprising result if one considers that sufficiently vegetated space provides a source of invertebrates (Turrini & Knop 2015), which are important as a food for the reproductive success of house sparrows (Peach et al. 2008; Seress et al. 2012). Moreover, woody plants (trees and shrubs) are important in providing shelter, especially for adult house sparrows during breeding season (Vincent 2005). Where green space is lacking, predation risk could increase and critically reduce small sparrow populations (Summers-Smith 2003). Most of the greenery cover in our study sites was represented by private gardens and individual trees outside of parks. Small urban green spaces, such as neighborhood parks and private gardens, have often been overlooked or considered unlikely habitat sources owing to their small size, even though they may nevertheless provide important nesting and food resources (Rega et al. 2015) and support house sparrow abundance. Therefore, even a relatively small loss of private gardens might have a large effects on sparrow abundance (Chamberlain et al. 2007). As in the case of backyard poultry, proportion of greenery cover has larger area in old build-up areas than in new built-up areas. Furthermore, due to the high price of land in new built-up areas, the majority of space in such areas is private and used for housing. Greater than 20% greenery cover was not recorded in any of the new built-up areas. The deficiency in adequate greenery cover together with low frequent poultry farming are therefore likely the most important factors causing significantly lower house sparrow abundances in new built-up areas.

Our results support suggestions by Shaw et al. (2008) that abundance of house sparrows could be linked to the socioeconomic status of humans inhabiting the settlements. Although recent urban development in the Czech Republic is driven by the same rules as elsewhere in Europe, there is a more obvious distinction between old and new areas because of changes in political and socioeconomic

systems since the 1990s. This difference is very discernible. Whereas in new built-up areas the people range from upper to middle-upper social classes, the classes continue to be mixed in older built-up areas. However, even though old buildings in the study area are not protected from modernization, they still sustain larger (traditional) houses compared with newly built houses which in result leads to significantly higher proportion of built up areas in old housing areas. Unfortunately, we found no sign of improvement with aging of new housing areas. Abundance of house sparrows was not higher in newly built-up areas developed before 2003 than in newer areas suggesting that the short-term aging process does not make modern housing more suitable for the species. Both types of built-up areas have similar road structures and traffic, so there is no difference in traffic emissions, which is one of the previously mentioned causes of house sparrow decline (Robinson et al. 2005). On the other hand, while old housing offers various nesting sites (e.g., roof cavities, old sheds, stacks of lumber), in new buildings all holes and cavities are covered and gardens are tidier, thus offering fewer nesting sites and shelter (Shaw et al. 2008). Although house sparrows are very flexible birds and the loss of one potential nesting area should not be crucial, the combination of several factors could be lethal (Summers-Smith 2003). We thus may expect that house sparrow decline will still continue as repairs to and replacement of old buildings in old-built areas will continue.

On the other hand, De Coster et al. (2015) found no association between house sparrow abundances and socioeconomic status of humans. They conducted their study, however, at the relatively broad scale of municipalities in Belgium. This scale is probably too coarse to detect such a relationship. Socioeconomic status differs within individual settlements and should be studied at a more detailed scale. As suggested by Seress et al. (2014) and Jerzak (2001), small-scale elements such as food resources (e.g., feeders, trash bins, backyard poultry) may be important to identify variables that influence distribution of bird including house sparrow. Such elements are difficult to map. We agree with Shaw et al. (2008) that the structure of socioeconomic status within settlements might stand as an important proxy for many other variables and thus could be used as an easy indicator of suitability of a settlement for house sparrow occurrence, albeit only at a small scale.

While several recently published studies often utilized citizen science data and have focused on patterns at a coarse scales (De Coster et al. 2015; Morrison et al. 2014), our study contributes to knowledge at a more local and finer scale by recording differences in environmental forces in the urban environment (Murgui & Macias 2010). Local studies should take into account the species' home range in studied areas. According to Peach et al. (2014), for example, house sparrows usually use

food sources within 30 m of their nests (with maximum distance of 165 m) and their home range decreases with increasing urbanization (Vangestel et al. 2010). House sparrow numbers in our study were shown to be independent of distance from older built-up areas. However, the distances achieved in average 50 m (maximum 650 m) in our sample which are distances easily accessible by house sparrows (De Laet et al. 2011). We suggest that more surveys with distances around 1 km and more between old and new built up areas are needed to help in better understanding the effect of site isolation on house sparrow numbers and occurrence.

Although nesting site opportunities for house sparrows could be increased by using artificial nesting boxes, such measures have been shown to have no effect on rural house sparrow abundance (von Post & Smith 2015). On the other hand, extending the green space in modern housing areas is important for many bird species, as well as for many other taxa generally (e.g., Hinsley & Bellamy 2000; Chong et al. 2014; Turrini & Knop 2015). Although parks are regarded as providing the main feeding habitat for house sparrows (e.g., Murgui & Macias 2010), we have shown that even solitary woody plants with sufficient density can play an important role for birds. In areas where planting trees and shrubs is not possible, green space could be increased by using green walls and roofs, which can increase the numbers of invertebrates, seeds, nesting sites, and shelters (Fernandez-Canero & Gonzalez-Redondo 2010; Chiquet et al. 2013).

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Chapter IV– Study 2

Title:

The role of the vegetation structure, primary productivity and senescence derived from airborne LiDAR and hyperspectral data for birds diversity and rarity on a restored site

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Abstract

Management of restored areas requires ecologically meaningful spatial data providing objective measures of restoration success. Understanding relationships between species diversity on the one hand and habitat heterogeneity and productivity on the other can help establish such measures and prioritize restoration management. We used airborne LiDAR and hyperspectral data to derive characteristics of vegetation structure, primary productivity and senescent vegetation (i.e. old dead vegetation) for prediction of richness and rarity of bird communities colonizing newly available habitats restored after coal mining. In addition, we analysed, which type of restoration (i.e. agricultural, forest, or spontaneous succession) results in more favourable conditions. The boosted regression trees explained 52% and 12% of deviance of overall species richness and rarity, respectively. We found that the overall species richness was strongly affected by the variance in vegetation structure, while the rarity was also affected by the presence of senescent vegetation. The relative importance of variables differed between the richness and rarity. The shrub cover had a strong positive effect on both, while the tree cover had a strong positive effect on species richness. The herbaceous cover and presence of senescent vegetation had positive effects on species rarity. This study, therefore, supports the necessity to create a mosaic of habitats with heterogeneous vertical structure including all layers of vegetation and highlights the importance of senescent vegetation. Combination of forests restoration with sites left to spontaneous succession appears to be the best strategy to increase both bird species richness and rarity in newly restored sites after coal mining.

Keywords:

Mining, NDVI, PSRI, Senescence, Spoil heap, Vegetation structure

Introduction

The mining of various raw materials has expanded globally in the last few decades with the growing demands for various commodities and their increasing consumption (Kung et al. 2020; Lébre et al. 2020). On the one side, economic benefits and wealth generated by the resource industry are substantial (Svobodova et al. 2020); on the other side, areas under mining lease are subject to significant landscape changes (Worlanyo & Jiangfeng 2020). The changes are often associated with negative environmental impacts, including irreversible land degradation and biodiversity loss (Giam et al. 2018; Osenberg 2018). However, under certain circumstances, mining and related activities can bring about also positive changes enhancing conservation value of the landscape (Šálek et al. 2010; Schulz & Wiegleb 2000; Vanhée & Devigne 2018).

Minimization of the negative effects of mining is typically ensured by ecological restoration, i.e. a process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Clewell & Aronson 2013; Martins et al. 2020). Monitoring of restored sites is required to gather ecologically meaningful data that can provide objective and quantitative measures of the restoration success. In practice, among other ecological measures, species diversity of various taxa is frequently used and many studies evaluated the effect of habitat heterogeneity on the diversity of species on restored sites (Crouzeilles et al. 2017; Martins et al. 2020). To model relationships between the species diversity and the heterogeneity of restored sites, however, the environment is usually represented by semiquantitative or categorical measures only (e.g. by rough subjective estimates of vegetation cover). Moreover, even these measures are usually spatially and temporarily limited as field surveys traditionally used by ecologists are extremely labour-intensive, especially over larger areas (Bejček 1988; Gould & Mackey 2015; Hagger et al. 2019; Kolář et al. 2017; Vojar et al. 2016). Although a direct field survey of habitat attributes can provide valuable information, it is unsuitable for repeated monitoring due to both labour intensiveness and limited informative value of subjective estimates, especially where detailed habitat characteristics are concerned.

In this study, we aim to identify measures that can be easily derived from airborne remote sensing data and used as a more elegant and more precisely measurable alternative to simple and subjective field surveys. Airborne remote sensing data are increasingly available from national or regional scanning campaigns (Melin et al. 2017; Stereńczak et al. 2020). Such technologies represent efficient and cost-

effective sources for developing indicators relevant to the large-scale decision making, to the understanding of continuous processes of site restoration, and developing effective management tools that will maintain high biodiversity of restored sites (e.g., Cordell et al. 2017; Laurin et al. 2020; Prošek et al. 2020; Urban et al. 2018). In addition, conservation strategies for post-industrial sites are highly debated in connection with restoration approaches (Hendrychová et al. 2020), including the adopted restoration method (Tropek et al. 2010; Vicentini et al. 2020; Vymazal & Sklenicka 2012). Therefore, we relate evaluated indicators to the individual restoration methods and provide recommendations for restoration practice.

In the next chapter, the theoretical background of the research and ecological explanation for the selection of environmental variables derived from airborne remote sensing data will be discussed and the aims of this study will be clearly expressed. Chapter 3 introduces the study area, the data and its preprocessing, the environmental variables and statistical analyses including models evaluation. Chapters 4 and 5 then present the obtained results followed by their discussion with respect to restoration goals and informing on possible limitations. Finally, the Chapter 6 contains conclusions and recommendations for restoration practice.

State of the art

Birds with their high dispersal ability play an important role in the early colonization of restored sites and therefore comprise one of the best indicators for the assessment of the restoration success (Bejček & Šťastný 1984; Cardoso da Silva & Vickery 2002; Martins et al. 2020). One of the important factors affecting bird species richness is the habitat heterogeneity. Habitat heterogeneity is determined by the variability of environmental conditions (e.g. habitat type, dominant vegetation species, soil types, topography) and it is assumed that more complex environments may provide more niches and thus increase species diversity (so-called habitat heterogeneity hypothesis; see review by Tews et al. 2004).

A common approach of indicating heterogeneity of the habitat is to use the variability in its physical structure (physiognomy) (Davies & Asner 2014). Physiognomy of the habitat is generally determined by plants and the debate whether bird species diversity is more affected by vegetation structure or by plant composition is still ongoing (Adams & Matthews 2019; MacArthur & MacArthur 1961; Müller et al. 2010). Although some studies have shown the importance of plant composition and it is clear that it should not be ignored (Adams & Matthews

2019), the vegetation structure has been traditionally considered the primary driver of bird diversity (Müller et al. 2010). This may be partly due to intensive research addressing relationships between bird richness and vegetation structure, which has been triggered by advances in the measurement of the vegetation structure by airborne LiDAR (see reviews by Davies & Asner 2014; Bakx et al. 2019).

Soon after the first studies showed the potential of LiDAR-derived vegetation structure for explaining species-environment associations, attempts begun to integrate LiDAR with variables derived using other complementary remote sensing data (e.g. multispectral or hyperspectral) assessing their relative importance and complementarity (Bae et al. 2018; Cooper et al. 2020; Goetz et al. 2007; Vogeler et al. 2014). Such variables include, for example, the normalized difference vegetation index (NDVI; Tucker 1979). The use of NDVI to model bird species richness is based on species-energy theory. According to that theory, species richness is limited by the quantity of available energy (Brown 1981; Wright 1983) and energy available to consumers is dependent on primary productivity (Evans et al. 2005). It is assumed that greater primary productivity of plants (i.e. biomass) supports higher animal species richness and NDVI is commonly used as a measure of vegetation productivity (Bailey et al. 2004; Hobi et al. 2017; Leyequien et al. 2007; Youngentob et al. 2015).

On the other hand, however, many species including birds are specialists and/or poor competitors, preferring specific habitats with relatively lower habitat heterogeneity or low primary productivity (Reif et al. 2016). The occurrence of these species can be associated with early stages of spontaneous succession, which are rare in the cultural landscape but relatively common on restored sites (Šálek 2012). These early successional habitats can, therefore, represent valuable refuges for rare and unique bird specialists and/or poor competitors.

For the early successional habitats in areas after coal mining, growths with old dead vegetation from previous vegetation season are typical (Hendrychová et al. 2020). This is particularly true for aquatic vegetation in areas left to spontaneous succession (e.g. *Phragmites australis* and *Typha latifolia*) but a similar representation of such old (dead) vegetation can be also observed in low steppe vegetation in agriculturally restored areas (e.g. *Calamagrostis epigejos* and *Arrhenatherum elatius*). For birds, the dead vegetation provides shelter, nesting, and foraging opportunities at the time when green vegetation is at minimal heights. It is, therefore, an important component of habitat heterogeneity not only in the autumn and winter but possibly even more so in the spring. The amount of old dead vegetation (i.e. senescent vegetation) can be estimated using the plant senescing reflectance index

(PSRI), which was developed as a quantitative measure of leaf senescence (Merzlyak et al. 1999) and used as a potential predictor of species occurrence in studies published previously (e.g. Soto et al. 2017).

Determining the attributes of the habitat heterogeneity and primary productivity of restored sites and their association with species diversity and/or rarity can help to identify ecologically valuable areas on large landscape scales. Therefore, in this study, we examined how the vegetation structure, primary productivity (i.e. NDVI) and old senescent vegetation from the previous season (i.e. PSRI) derived from airborne laser scanning and hyperspectral data predict species richness and rarity of bird communities colonizing newly available (restored) habitats after coal mining. Specifically, we focused on the following questions: (i) Is there a detectable relationship between the fine-scale habitat attributes of early succession stages obtained by airborne remote sensing and the occurrence of birds? (ii) Which is of greater importance for the occurrence of birds – the primary productivity, presence of old vegetation, or vegetation structure? And (iii) which type of restoration (i.e. agricultural, forest, or spontaneous succession) results in the development of more favourable habitats for bird species richness and rarity?

Data and methods

Study area, type of reclamation and habitats

The study was carried out on the Radovesická spoil heap (Fig. 1) located in the North Bohemian Brown Coal Basin, Czechia, one of the largest active brown coal mining regions in Europe. The study area was subject to various methods of restoration (i.e. agricultural, forestry, and spontaneous succession; Fig. 2). Agricultural reclamations typically include the establishment of permanent grasslands with initial sowing of a species-poor grasses mixture (*Festuca, Dactylis, Phleum, Poa, Cynosurus, Agrostis*) mixed with about 10% of legumes (*Trifolium, Coronilla, Lotus, Medicago*). Such areas are mowed twice a year even after the reclamation is completed. Afforestation includes predominantly homogenous plantations of even-aged stand combining autochtonous and allochthonous trees (*Acer, Pupulus, Quercus, Fraxinus, Tilia, Carpinus, Larix*) supplemented with shrubs (*Eonymus, Padus, Lingustrum, Cornus, Symphoricarpos, Spiraea, Lonicera, Viburnum*).

Successional sites in our study area are characterized by structurally diversified bare ground with sparse annuals and biennials, followed by perennials (*Tanacetum, Artemisia, Cirsium*) and grasses (especially *Calamagrostis epigejos* and *Arrhenatherum elatius*) with scattered authochtonous shrubs (*Sambucus, Rosa, Betula, Crataegus*). The tree growths on the successional sites are dominated by birch (*Betula pendula*), mixed with other deciduous trees (*Salix, Populus*). See Fig. S1 in the Supplementary material for examples of vegetation structure.

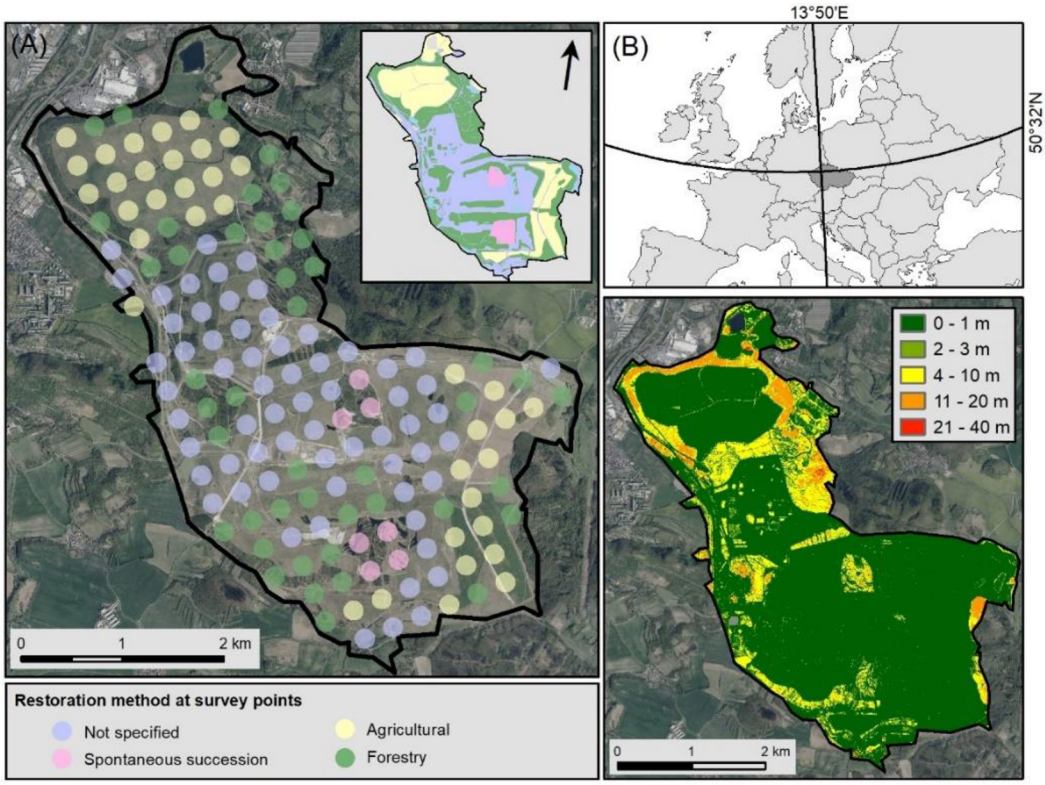

Fig. 1. Study area; (A) Location of survey points and adopted restoration method (forestry, agriculture, and naturally regenerating systems called "spontaneous succession"). The survey points represent a 100 m buffer; (B) Location of the study area in the Czech Republic; (C) Canopy height model (meters).

Fig. 2. Aerial photos of the study area. The two photos in the top row were taken on the 10th of May 2020 and show the two areas left to spontaneous succession surrounded mostly by agriculturally restored areas. The three bottom images were taken on 25th of April 2020 and show the areas after agricultural restoration (left), forest restoration (middle), and the area left to spontaneous succession (right). Note the presence of old dead vegetation even at this time of the year, particularly in areas left to spontaneous succession, near water bodies and other terrain depressions.

Bird survey, richness and rarity calculation

Bird data were collected in 2012 by five experienced ornithologists (co-authors of this study). Each of the 153 survey points was visited twice during the season (5–6 and 28–29 May) to increase the likelihood of detecting the earlier and later breeding species. The survey points form a grid spaced at 300 m intervals. At each survey point, all bird individuals identified by sight or sound within a 100 m distance from the survey point were recorded. The results from both visits were pooled together and the bird diversity (species richness) for each survey point was calculated as the number of species detected on the survey point. In addition, we calculated an index of species rarity for each survey point reflecting the scarcity of species throughout the Czech Republic based on the large-scale quadrat mapping of birds (Šťastný et al. 2006). For each species, the rarity index was calculated using the formula $1-N/628$ where N represents the number of quadrats occupied by the species from 628 in total (Šálek 2012; Table S2 in Supplementary material). The overall rarity for each survey point was then calculated as the sum of index values

for all species recorded at a point. Individuals recorded while flying over the site or beyond the defined distance were excluded from the analysis.

Airborne data collection and pre-processing

The airborne LiDAR and hyperspectral data were acquired simultaneously on 18th May 2017 using a remote sensing platform FLIS (The Flying Laboratory of Imaging Spectroscopy; Hanuš et al. 2016). Flights for data collection were conducted at 1030 m above ground at 110 knots (ground speed). Data from the hyperspectral (Visible Near Infrared, VNIR, CASI-1500), and LiDAR sensor (Riegl LMS Q-780) were used in this study. Although there was a time lag between the field survey and LiDAR and hyperspectral data campaign, we assume that data were still useful for describing birds' habitats in terms of vegetation structure, vegetation productivity and presence of old dead vegetation as it has not changed substantially over the five years (but see more on this topic in Discussion).

Hyperspectral data

The hyperspectral imagery consisted of 48 bands covering the visible near-infrared range from 380 to 1050 nm (CASI-1500) with a bandwidth of 7.2 nm. Pre-processing of the hyperspectral images (i.e., radiometric correction, georeferencing and atmospheric corrections) were all carried out by the provider (CzechGlobe). Radiometric corrections were performed in the RadCorr software by converting spectral radiances to physical radiance units based on calibration parameters from the CzechGlobe spectroscopic laboratory (Hanuš et al. 2016). Radiance images were geometrically corrected, orthorectified using a digital terrain model (DTM), and georeferenced to the local Datum of Uniform Trigonometric Cadastral Network (EPSG: 5514). Data were corrected for atmospheric conditions using a radiative model MODTRAN and the BREFCOR method was used for correcting the bidirectional reflectance distribution function (BRDF) effect (ATCOR-4 software; Richter & Schläpfer 2016).

LiDAR data

Airborne LiDAR data were acquired with a Riegl LMS Q-780 laser scanner. The scanner has a rotating polygon mirror and scans in parallel lines. The scan field of view is 60° and the wavelength is 1064 nm. The LiDAR data were provided in LAZ format with an average point density of 8 points per square meter. The

LiDAR point cloud was processed using a proprietary software by the Global Change Research Institute CAS and referenced to the local Datum of Uniform Trigonometric Cadastral Network (EPSG: 5514) and Baltic Vertical Datum – After Adjustment (EPSG: 5705). We further processed the point cloud using LAStools (http://lastools.org) and classified the point cloud into ground and vegetation classes (Klápště et al. 2020; Moudrý et al. 2020). We divided the study area into 36 tiles and classified each tile separately to allow different settings and thus a better identification of ground and vegetation returns. In addition, we identified noise returns (e.g. returns from birds) and within the distance of 100 m from the grid survey points, we manually checked and edited point clouds for obvious errors (e.g. high voltage poles classified as vegetation). Returns other than vegetation and ground were removed from subsequent analyses. Prior to the calculation of vegetation structure variables, we height-normalized the LiDAR point cloud (i.e. the returns' height above the DTM was calculated).

Primary productivity and habitat heterogeneity variables

To investigate the importance of primary productivity and habitat heterogeneity, we derived two vegetation indices from the hyperspectral data and six variables from the LiDAR data; all these indices and variables bear a potential relevance to the bird diversity (Table 1). The two calculated vegetation indices included 1) NDVI (R862 - R662)/(R862 - R662), which corresponds to plant chlorophyll content and hence increases with vegetation productivity (i.e. the green component of biomass), and 2) PSRI (R678 - R500)/R750, which is a measure of the leaf senescence and is sensitive to the carotenoid/chlorophyll ratio. PSRI is in this study used as an estimate of the amount of old dead (senescent) vegetation from the previous vegetation season, which is present in the study area even in May when both bird and airborne data were collected (see Fig. 2). The old dead vegetation from the previous season is mainly present in the aquatic vegetation (e.g. *Phragmites australis* and *Typha latifolia*) and, to a somewhat lesser extent, in low steppe vegetation (e.g. *Calamagrostis epigejos* and *Arrhenatherum elatius*).

In order to assess the effect of habitat heterogeneity on bird species richness and rarity, we described habitat heterogeneity using the variance in vegetation structure. We used vegetation structure variables adopted in the previous bird diversity studies (see Bakx et al. 2018 for the conceptual categorization of LiDAR-derived vegetation metrics). To describe the total vegetation (*sensu* Bakx et al., 2018) we used the mean, standard deviation of vegetation returns, and canopy cover (Table 1). We calculated these metrics to describe the structural variability

of the vegetation directly from the point cloud (e.g. Bae et al. 2018); but note that some other studies calculated these metrics from the rasterized canopy height model (CHM) to describe a horizontal variation in the canopy cover (e.g. Müller et al. 2009; 2010). In addition, we used variables characterising the individual vegetation layers (single layer *sensu* Bakx et al. 2018). Three layers of vegetation are typically recognized; the herbaceous layer, the shrub layer, and the tree layer (e.g. Lesak et al. 2011; Jones et al. 2013). The same vegetation layers are typically assessed during field inspections on postmining sites (e.g. Šálek 2012). Therefore, we calculated the cover for three vegetation layers: first, we counted the number of points between 0.1 m and 1 m and divided this number by the sum of all points to estimate the cover of the herbaceous layer. Second, we counted the number of points between 1 m and 3 m and divided the result by the sum of all points to estimate the cover of the shrub layer. In the same way, the number of points between 3 m and 40 m was divided by the sum of all points to estimate the cover of the tree layer (in our study area, there are no trees higher than 40 m). It should be noted that the heights of these vegetation layers are selected arbitrarily based on our field experience (e.g. Šálek 2012) and can thus greatly vary among different areas (e.g. Lesak et al. 2011). All primary productivity and habitat heterogeneity metrics were calculated within a 100 m radius of grid survey points using ENVI (version 5.5) and LAStools (version 200112), respectively.

Statistical analyses

We used boosted regression trees (BRT) implemented in the R package gbm version 2.1.5 (Greenwell et al. 2019) and some additional features available in the package dismo version 1.1–4 (Hijmans et al. 2017) to assess how primary productivity and habitat heterogeneity were associated with species richness and rarity. First, we examined the collinearity among all variables to reduce the number of input variables (Fig. S3 in Supplementary material). Canopy cover and mean height were highly correlated with vertical vegetation structure metrics. As it has been highlighted that birds show a higher preference for the structural variability of the vegetation than for canopy cover (Davies & Asner 2014) and as the vertical vegetation variability was of our primary concern, we retained the three vertical layers (i.e. herbaceous, shrub and tree cover) and excluded the canopy cover and mean vegetation height from further analyses. Another highly correlated pair of variables were NDVI and PSRI; however, as they represent unique components of the aboveground biomass and were essential for our study, we decided to retain both variables in the model. However, to evaluate whether retaining both NDVI and PSRI affected our results, we ran the models also individually with PSRI and

NDVI, respectively (see the Supplementary material, Figs. S5–S8). Therefore, our final set of variables consisted of four variables representing the habitat heterogeneity and two variables representing the primary productivity (Table 1).

Table 1 - Overview of 8 potential explanatory variables derived from LiDAR and hyperspectral data within a 100 m vicinity of survey points. Rx denotes the reflectance at the wavelength of x nm. We excluded areas of water bodies from calculations of NDVI and PSRI. Variables in bold were used in our final models (i.e. after excluding collinear variables)

Hyperspectral and LiDAR derived metrics	Description	Category according to Bakx et al. (2020)
Primary productivity		
Normalized Difference Vegetation Index (NDVI)	$(R_{862} - R_{662})/(R_{862} - R_{662})$; sensitive to vegetation greenness	-
Old dead vegetation from the previous vegetation season		
Plant senescing reflectance index (PSRI)	$(R_{678} - R_{500})/R_{750}$; sensitive to senescent vegetation	-
Vegetation structure (Total vegetation)		
Mean height	Average height of vegetation returns	Total vegetation - Height
Standard deviation of height	Standard deviation of vegetation returns heights above 1m	Total vegetation - Vertical variability
Canopy cover	Number of first returns above 1m divided by the sum of all first returns	Total vegetation - Cover
Vegetation structure (Single layers)		
Cover of herbaceous layer	Number of points between 0.1m and 1m divided by the total number of points	Single layer (Understorey) - Cover
Cover of shrub layer	Number of points between 1m and 3m divided by the total number of points	Single layer (Understorey) - Cover
Cover of tree layer	Number of points >3m divided by the total number of points	Single layer (Canopy) - Cover

Two most important parameters that need to be specified for BRT are the tree complexity (which controls whether interactions are fitted) and learning rate (shrinkage) as they determine the number of trees required for the prediction. As a rule of thumb, a combination of tree complexity and learning rate that results in

a model with at least 1000 trees is recommended. For models with less than 500 records, it is preferred to model simple trees (i.e. tree complexity 1–3) with a small learning rate to allow the model to grow enough trees. We fine-tuned the settings in preliminary testing and used models with tree complexity (the number of splits in a tree) of 1 (i.e. without interaction terms, as allowing interactions did not lead to a model improvement), shrinkage (learning rate) of 0.001, bag fraction (the proportion of data used when selecting optimal tree number) of 0.5, and the maximum number of trees of 5000. To estimate the optimal number of trees, we used 10-fold cross-validation. At each iteration, the residual deviance was calculated and the number of trees giving the best model (i.e. lowest deviance) was identified (Elith et al. 2008; Hastie et al. 2001; Leathwick et al. 2006). Species richness and rarity were modelled specifying the Poisson and Gaussian error distribution, respectively. All models were fitted in R, version 3.6.0 (R Development Core Team, 2019).

Assessment of model performance

The identified best models were fitted to the entire dataset and used to produce partial dependency plots that show the effect of each variable after accounting for the average effects of all other variables (De'Ath 2007; Elith et al. 2008). In addition, we assessed the relative importance of each variable (i.e. the contribution of each variable to the model fit scaled so that the sum adds to 100) using formulae developed by Friedman (2001) and implemented in the gbm package (Greenwell et al. 2019). The overall performance of BRT models was evaluated using the total deviance explained, which was calculated by dividing the difference between the mean total deviance and the estimated 10-fold cross-validated residual deviance by the mean total deviance. The cross-validated residual deviance is a measure of the deviance left unexplained by the model. Because results from the k-fold cross-validation can vary depending on the random selection of points for the folds, this procedure was repeated 5 times for each model, and overall means were calculated for the relative importance of each variable and total deviance explained by the models (Leathwick et al. 2006).

Results

Bird richness

We observed 83 bird species from a total of 1340 individual bird records. The overall bird species richness ranged from 1 to 17 species per survey point with a median of 6 species (Fig. 3). The BRT model of overall species richness explained 52% of deviance. The overall species richness was strongly affected by the habitat heterogeneity while primary productivity had only a minimal effect (Table S4 in Supplementary material). The effects of the midstory density and canopy density were the strongest and jointly accounted for most of the explained variability. The standard deviation of height had a moderate effect, and the effects of herbaceous cover, NDVI and PSRI were weak (Fig. 4). The partial dependency plots of the individual variables showed a rapid increase of species richness at relatively low values of the shrub cover and tree cover with only a minimal change as these variables continued to increase. The ranges of the shrub cover and herbaceous cover associated with the steepest increase in the bird richness were 0–5% and 0–20%, respectively. The standard deviation of height had a positive effect with an increase in overall richness for values between 2 m and 3 m and no effect above that value (Fig. 4).

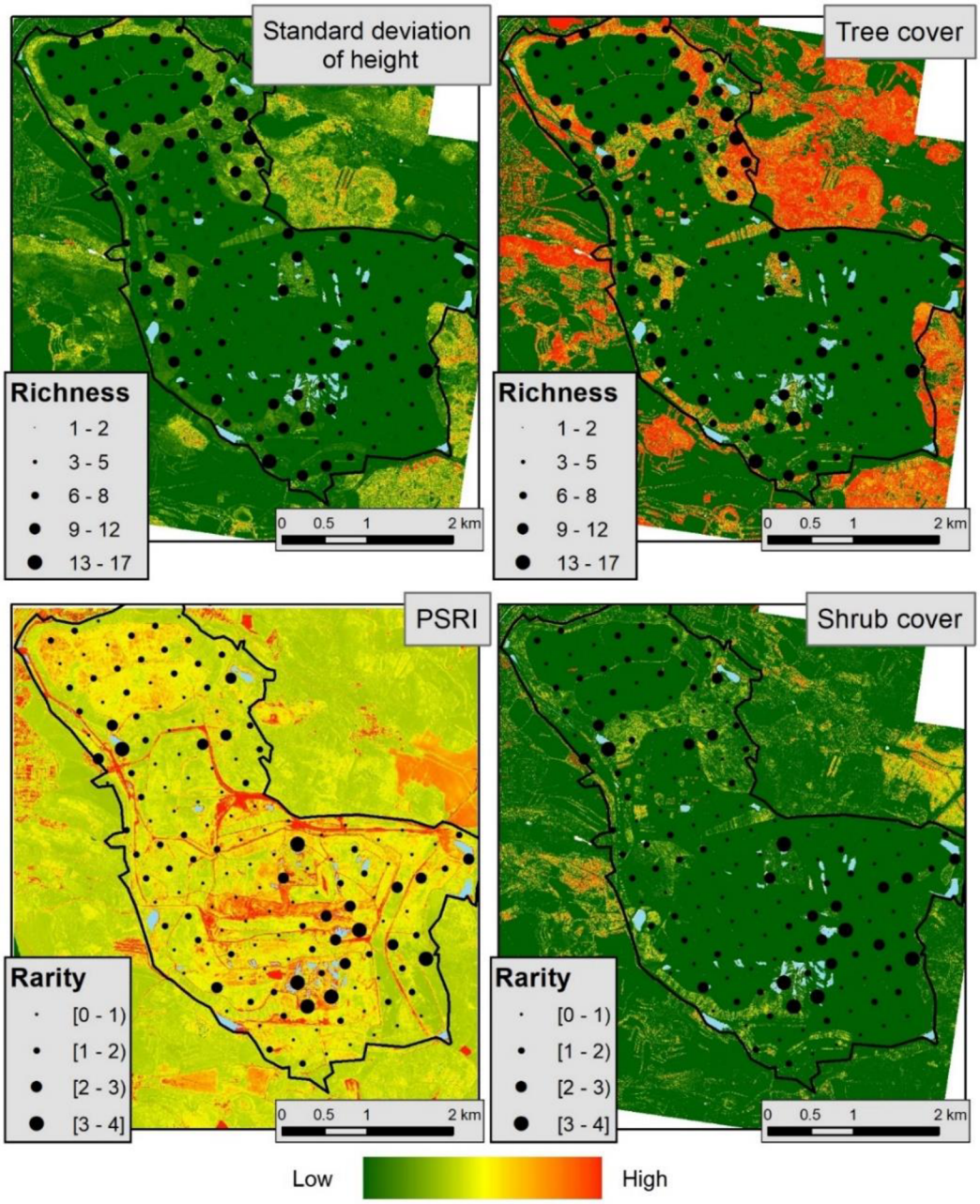

Fig. 3. Spatial distribution of species richness (upper images) and rarity (lower images) along with the four most influential explanatory variables (Standard deviation of height, Tree cover, PSRI, and Shrub cover).

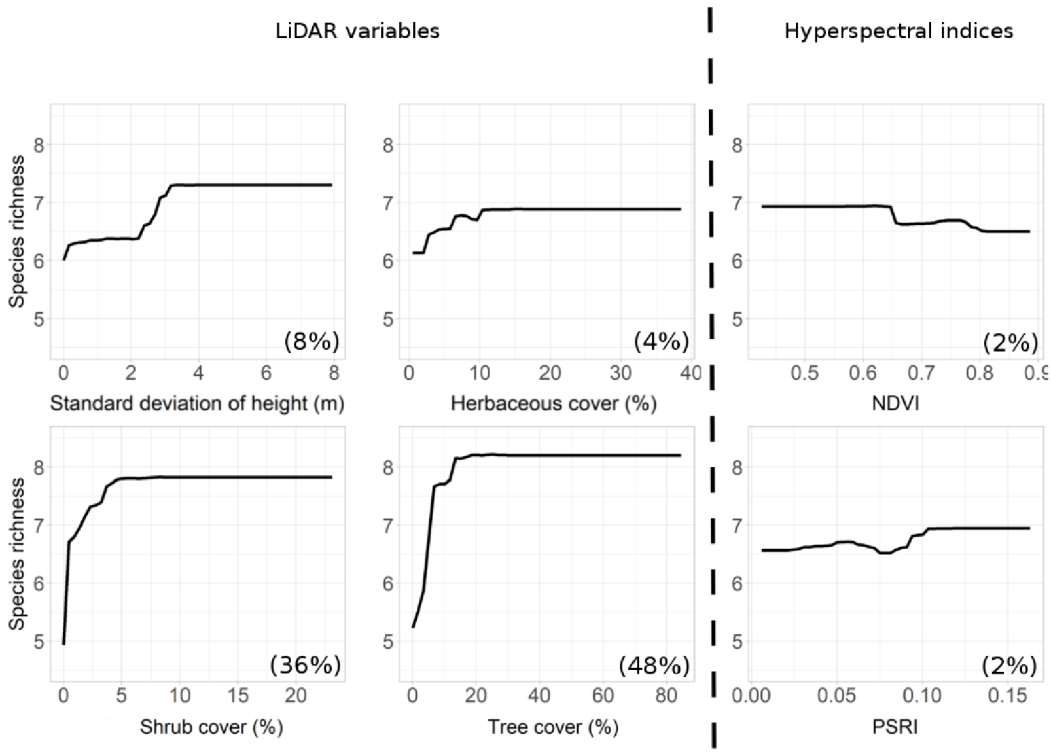

Fig. 4. Partial dependency plots for boosted tree analyses of overall species richness. The partial plots show the modelled relationships between species richness and standard deviations of height, herbaceous cover, shrub cover, tree cover, NDVI, and PSRI. The relative importance of the variable in the model is given in parentheses.

Bird rarity

The bird rarity index ranged from 0.04 to 3.81 per survey point with a median rarity of 1 (Fig. 3). The BRT model of bird rarity explained 12% of deviance and the rarity was strongly affected by both habitat heterogeneity and primary productivity (Table S4 in Supplementary material). The shrub cover, herbaceous cover and PSRI had the strongest effects and jointly accounted for most of the explained variability. The effects of the standard deviation of height and NDVI were moderate, and the canopy density had a weak effect (Fig. 5). The partial dependency plots of the single variables showed a rapid increase in rarity for PSRI values above 0.10. A rapid increase in rarity was also shown at relatively low values of shrub cover and herbaceous cover with a minimal change as these variables continued to increase. The ranges of the shrub cover and herbaceous cover associated with the steepest increase of the bird rarity were 0–5% and 10–15%, respectively (Fig. 5).

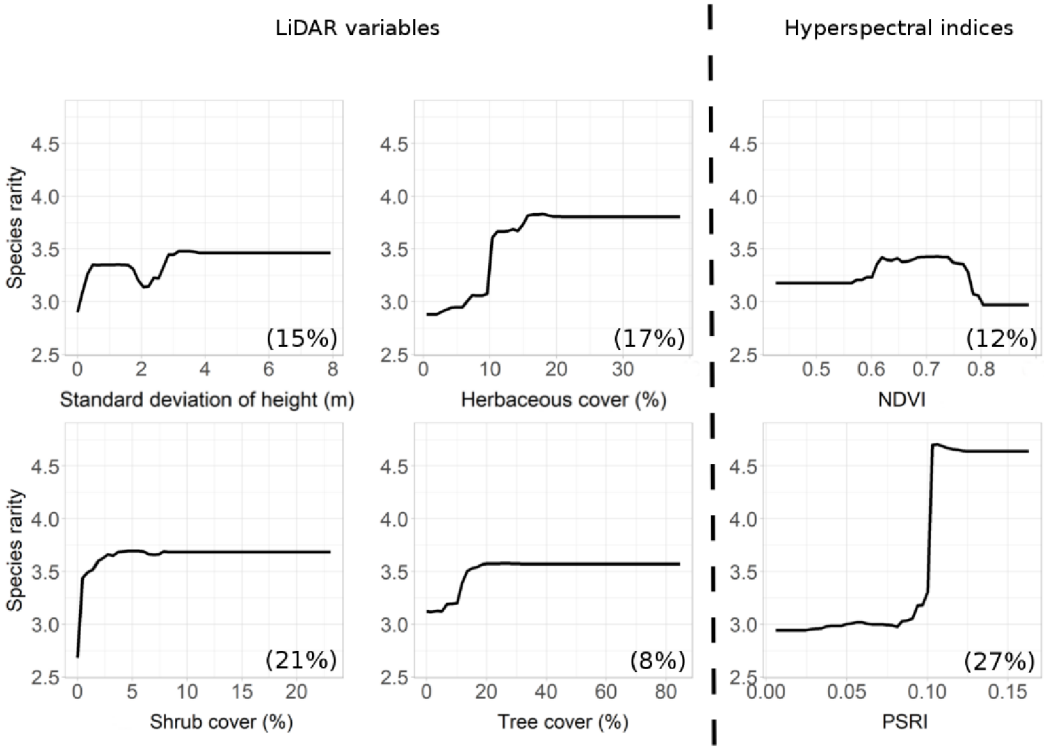

Fig. 5. Partial dependency plots for boosted tree analyses of species rarity. The partial plots show the modelled relationships between the species rarity and standard deviations of height, herbaceous cover, shrub cover, tree cover, NDVI, and PSRI. The relative importance of the variable in the model is given in parentheses.

Heterogeneity and productivity with respect to the restoration technique

Our results show a clear effect of the adopted restoration technique on habitat heterogeneity and primary productivity (Fig. 6). Most importantly, the spontaneous succession considerably differs from other sites when looking at primary productivity. The values of NDVI (i.e. vegetation greenness) and PSRI (i.e. senescent vegetation) were relatively similar for the agricultural and forest restoration but compared to them, the sites left to spontaneous succession had much lower values of NDVI and clearly higher values of PSRI (Fig. 6). The structural measures show a distribution of values commensurate with the individual habitat types. Note that the sites with unspecified restoration method were similar to agricultural restoration and mostly consisted of low vegetation.

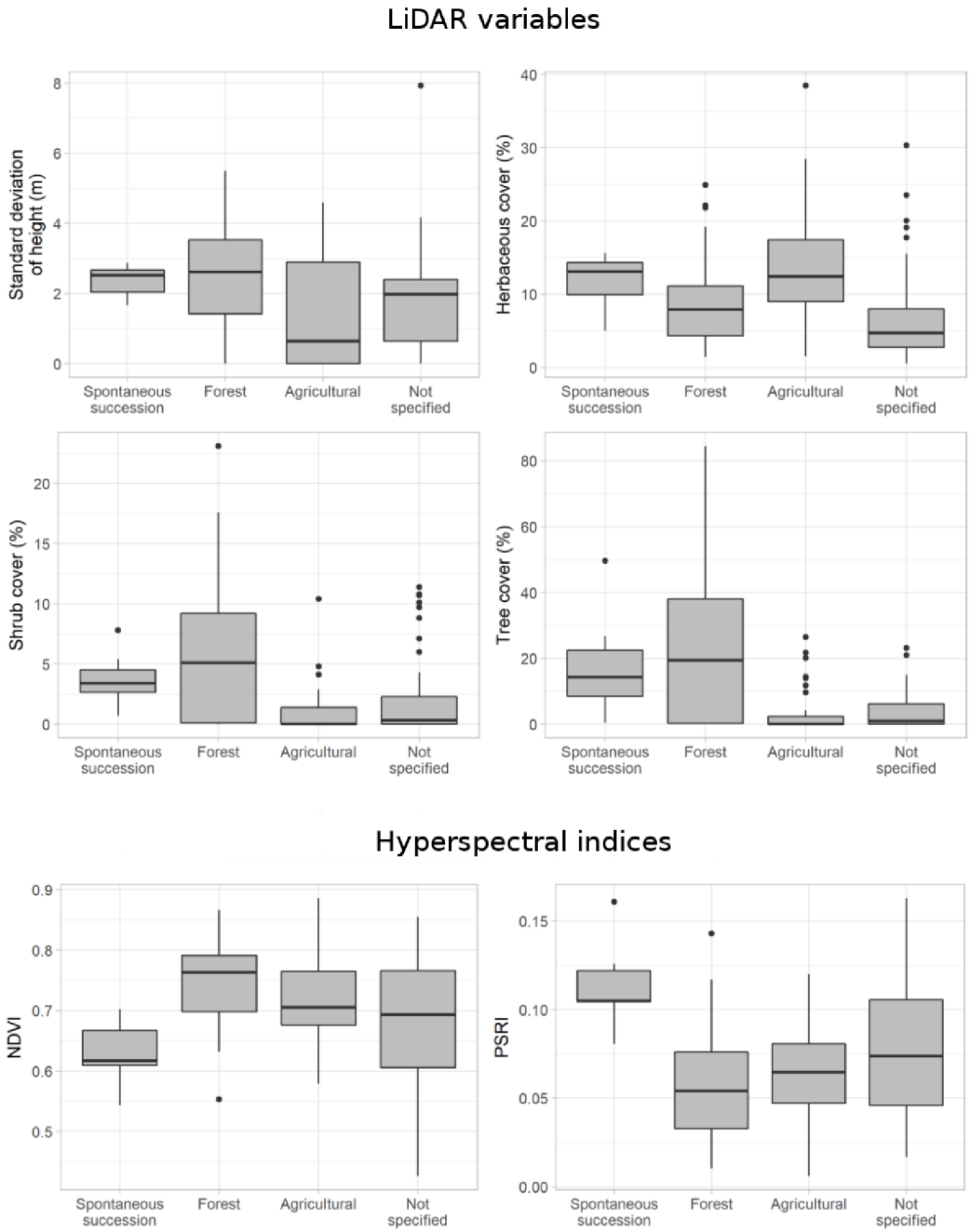

Fig. 6. Comparison of vegetation structure (LiDAR variables), NDVI and PSRI indices depending on the adopted restoration techniques. The central horizontal line in the box marks the median. The boxes show the interquartile range (25th to 75th percentile) and the whiskers indicate 1.5 times the interquartile range.

Discussion

In this study, we evaluated the effect of the variance in vegetation structure, primary productivity and senescent vegetation on bird communities colonizing newly available (restored) habitats after coal mining (Fig. 3). We found a detectable relationship between fine-scale habitat attributes of early succession stages derived from airborne LiDAR and hyperspectral data and the occurrence of birds. The models with six variables representing the vegetation structure, primary productivity and the presence of senescent vegetation explained 52% and 12% of the variability in species richness and rarity, respectively, which is comparable to prior studies. The previous studies combining LiDAR data with the indices derived from passive optical sensors (e.g. NDVI) typically explained the variability in species richness between 15% and 55% (Goetz et al. 2007; Jones et al. 2013; Vogeler et al. 2014).

Importance of vegetation structure, NDVI and PSRI for bird species richness

Variance in vegetation structure had a positive effect on species richness and explained most of the explained variability (Fig. 4). While NDVI and PSRI showed almost no effect on species richness, shrub cover (i.e. the cover of shrubs and saplings between 1 m and 3 m high) and tree cover (i.e. cover of vegetation >3 m high) exhibited a strong positive effect on species richness. The standard deviation of height and herbaceous cover (cover of vegetation up to 1 m high) had minor effects on species richness. Species richness climbed steeply at low values of shrub cover (0%–5%), low values of tree cover (0%–20%), and the standard deviation of height between 2 m and 3 m (Fig. 4). Such conditions are typical of forest restoration and sites left to spontaneous succession (Fig. 5). These findings are in accordance with prior studies such as Goetz et al. (2007) and Vogeler et al. (2014) who combined LiDAR with NDVI and more recently Melin et al. (2019) who combined LiDAR with variables derived from hyperspectral data and showed that the vegetation structure (i.e. LiDAR derived variables) is more important for the assessment of bird species richness at local scales than variables derived from passive remote sensing.

Importance of vegetation structure, NDVI and PSRI for bird species rarity

In contrast to species richness, our results show that combining information from LiDAR and passive optical sensors might be important when species rarity is of concern. We found a positive effect of both habitat heterogeneity and primary productivity on species rarity (Fig. 5). PSRI (i.e. old dead vegetation from the previous vegetation season) was the most important predictor with a strong positive effect on species rarity, followed by shrub and herbaceous cover. The greatest increase in rarity was associated with PSRI values higher than 0.10, above 2% for the shrub cover, and above 10% for the herbaceous cover (Fig. 5); above these values, the rarity remained more or less constant. This is likely because the senescent vegetation and relatively high herbaceous and shrub covers provide shelter and enhance the diversity of insect communities and hence food availability for birds (e.g. Müller et al. 2014; Soto et al. 2017; Vergara et al. 2017).

It is, however, important to note that the model of bird rarity explained only 12% of deviance. This is likely related to the fact that typical rare species that occur in our study area are ground-nesting or foraging birds. Such species include, for example, Wheatear *Oenanthe oenanthe*, Montagús Harrier *Circus pygargus*, Bluethroat *Luscinia svecica cyanecula*, Whinchat *Saxicola rubetra*, Stonechat *Saxicola torquata*, Great Reed Warbler *Acrocephalus arundinaceus* or Meadow Pipit *Anthus pratensis*. These specialists require specific and mutually different conditions such as bare grounds (Wheatear), unmanaged grassy patches (Montagús Harrier, Whinchat, Stonechat, Meadow Pipit) or reedbeds (Bluethroat, Great Reed Warbler) that are neither adequately represented by the variance in the vegetation structure nor by NDVI and PSRI indices, respectively. Indeed, ground-nesting or foraging species are typically reported to be poorly modelled using habitat heterogeneity and productivity variables (Cooper et al. 2020; Weisberg et al. 2014). The five-year time lag between the data acquisitions and difficulties to distinguish old dead vegetation from bare surfaces might represent alternative explanations for the relatively low deviance explained by these factors (see Chapter 5.4. below).

Which type of restoration results in the development of more favourable habitats?

It is evident that all vertical levels of habitat heterogeneity (i.e. herbaceous, shrub and tree covers) are important either for species richness or rarity. This supports the necessity to create the mosaic of habitats with heterogeneous vertical structure

during restoration to support high species richness as suggested e.g. by Harabiš et al. (2013). However, the high variance in vegetation structure alone is not sufficient to support rare species. Indeed, management and restoration goals can change considerably depending on whether the aim is to support high species richness or rare species (Cooper et al. 2020). It seems that a high herbaceous and shrub cover combined with the presence of old dead vegetation promote rarity. However, this combination is rare on technically reclaimed sites, i.e. after agricultural and forest restoration. In contrast, this study shows that such conditions are typically present on sites left to spontaneous succession (Fig. 5). This is a likely explanation for the fact that the spontaneous succession sites are particularly favoured by rare vertebrates (Šálek 2012; Vojar et al. 2016).

Use and limitations of airborne remote sensing data in restoration practice

We have shown that the measurement of the habitat heterogeneity derived from airborne laser scanning point clouds can provide ecologically meaningful variables. As field-based estimates of vegetation structure are used as a rapid and efficient way of assessing the condition of restored sites (Gibbons & Freudenberger 2006), LiDAR can become an alternative to such field surveys. Compared to field surveys, however, LiDAR has a higher potential for providing information that can lead to management action. As LiDAR data availability is increasing continuously due to national or regional scanning campaigns (see Melin et al. 2017; Stereńczak et al. 2020 for the list of countries and regions with LiDAR data available) and thanks to the more common adoption of open data policies (Rocchini et al. 2017), there is a high potential to use it in restoration ecology, especially for assessment of vegetation structure (Guo et al. 2017; Koska et al. 2017; Moudrý et al., 2019; Moudrý et al. 2019; Szostak et al. 2020). Therefore, we suggest that such data should be increasingly utilized by managing authorities for optimizing the restoration success assessment and enhancing the ecological value of reclaimed areas.

It should be, however, noted that despite the increase of LiDAR data availability, acquisitions for the same area (e.g. state) have, due to high acquisition costs, long repetition times. Therefore, studies such as the presented one are often being done under suboptimal conditions and the time lag between field surveys and LiDAR data acquisition is common (Lesak et al. 2011). For example, Goetz et al. (2007) – 6 years; Wallis et al. (2016) – 10 years. Huber et al. (2016) – 10 years. It has been shown that several years time lag is not a fundamental source of error in mature woodland ecosystems as the changes in vegetation structure are usually relatively

slow (Hill & Hinsley 2015; Vierling et al. 2014). This is, however, not the case of our study area that consists of agricultural, forest, and successional sites and the time lag between remotely sensed and bird data collection might be a potential source of error. While this is certainly not a problem for agriculturally restored sites, differences in vegetation structure might have arisen during the 5 years at sites restored through forestry and those left to spontaneous succession. On the other hand, the two sites left to spontaneous succession in our study area are 16 and 26 years old, respectively, and the current rate of changes in the vegetation structure is relatively slower than during the early stages of succession. Moreover, the spontaneous succession is often blocked by sandy soils and dense grass cover (e.g. *Calamagrostis epigejos*). Therefore, the main differences can be expected in vegetation within the 1 – 3 m height range that could have grown over 3 m.

It is even more important to minimize the time lag when hyperspectral data are used. This is especially true when indices related to the vegetation biochemistry (which can change in a matter of weeks across a vegetation season) are used, it is much preferable if the hyperspectral data collection and bird survey are performed at the same time (e.g. Melin et al. 2019). Whit this in mind, we did not use any indices related directly to vegetation biochemistry and concentrated only on indices that are positively correlated to the characteristics that should have remained relatively stable over the five years (i.e. NDVI for vegetation productivity and PSRI for the amount of old dead vegetation). Besides, the bird occurrences and remotely sensed data were both collected in May, which was particularly important for the ecological relevance as this allowed accurate estimates of the amount of old dead vegetation present during the breeding season. The old dead vegetation is typical for terrain depressions (e.g. *Phragmites australis* and *Typha latifolia*) and agriculturally restored areas (e.g. *Calamagrostis epigejos* and *Arrhenatherum elatius*) and its detectability is changing more within a year than between years due to the pronounced seasonality (see also the note above on blocked succession). The amount of old dead vegetation is actually constantly growing and such sites might have become even more favourable for rare species as Whinchat, Stonechat, Montagús Harrier or Bluethroat in 2017 (the year of remote sensing data acquisition) than they were in 2012 (the year of bird data collection).

There is, however, another potential source of error, which might possibly also have been the reason why the model of bird rarity explained only 12% of deviance, namely the fact that the PSRI is high also in areas completely without vegetation, such as roads (Fig. 2). On the other hand, however, old dead vegetation, which forms an important habitat for Whinchat or Stonechat, is often present in the

ditches along the roads (e.g. *Arrhenatherum elatius*) and it is, therefore, difficult to separate their effects.

For future studies and especially for monitoring practice, it would be beneficial to agree on several LiDAR-derived metrics proven to be effective for explaining species diversity and to recommend them as standard structural indicators. To facilitate comparisons, Bakx et al. (2019) recently grouped LiDAR-derived variables into 24 classes defined by six categories of vegetation (total vegetation, single trees, canopy, understorey, other single layers, and multi-layer) and four categories of the structural type (cover, height, horizontal variability and vertical variability). Our results show that the total vegetation vertical variability (i.e. standard deviation of returns height) and canopy and understory cover (i.e. herbaceous, shrub and tree covers) are potentially relevant for the assessment of conditions on early successional restored sites.

Conclusions

Understanding drivers of species distributions across restored landscapes and identifying areas that have the potential for supporting high species richness, vulnerable or rare species, is important for successful management of restored sites. Overall, our results show that both habitat heterogeneity and primary productivity play an important role in bird species diversity on restored sites. Shrub cover had a strong positive effect on both species richness and rarity, while tree cover had a strong positive effect on species richness. Herbaceous cover and the presence of senescent vegetation had both positive effects on species rarity. This highlights the necessity of creating a mosaic of habitats with heterogeneous vertical structure during restoration or to design the vegetation structure in a way supporting preferred species. To support this, we suggest to reduce intensive mowing of agriculturally restored areas (e.g. by creating unmowed strips of vegetation), preserve naturally formed waterlogged areas, plant trees with different growth rates and combine them with shrub vegetation. Sites left to spontaneous succession play an important role in creating restored ecosystems of high ecological value as they represent a unique combination of vegetation density and presence of senescent vegetation that, in combination, promote high species rarity.

In our opinion, airborne remote sensing, particularly laser scanning, should constitute an integral part of restoration success assessment and should be

acquired with reasonable repetition rate (e.g. 5–10 years) over the restored areas, as the information derived from such data can be more easily implemented in management actions than subjective semiquantitative or categorical measures collected during intensive fieldwork. We suggest a wider use of vegetation structure and productivity indices derived from remotely sensed data in restoration success assessment. Our results show that the total vegetation vertical variability (i.e. standard deviation of returns height) and various vertical layers of vegetation cover (i.e. herbaceous, shrub and tree cover) in combination with senescent vegetation (i.e. PSRI) are potentially relevant for monitoring of early successional restored sites.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2021.104064.

Chapter V – Study 3

Title:
Habitat heterogeneity derived from lidar and hyperspectral data in a restored site and its surroundings: Implications for bird guilds and restoration management

Authors:

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Author's contribution:

Conceptualization, Data Curation, Methodology, Writing - original draft, Writing - review and editing

In review in the Journal of Applied Ecology

Abstract

A global transition of energy production is underway. Coal-based power production is gradually being replaced by renewable energies, leading to the decommissioning of coal-mining sites. In Europe, this presents an opportunity for restoring degraded habitats, in alignment with the goals of the Nature Restoration Law. However, systematic approaches to monitoring of restoration of mining sites are lacking as current practices are often labour-intensive, and (both spatially and temporally) constrained. In this study, we evaluated the suitability of habitat heterogeneity metrics derived through airborne remote sensing for monitoring of coal-mining site restoration. Specifically, we tested the response of guild-specific bird species richness to various metrics of habitat heterogeneity, both at and around a restored coal-mining site. We (i) examined differences in habitat heterogeneity, including terrain, vegetation structure, and senescent vegetation, between restored and surroundings areas; (ii) documented key aspects of habitat heterogeneity that influence the richness of birds with diverse ecological requirements (i.e. guilds), and (iii) tested for significant differences among bird responses between restored and surrounding areas. Generalised additive models explained between 19% and 78% of the variability in guild richness. Canopy cover, understory cover, the standard deviation of vegetation height, and senescent vegetation positively affected overall bird diversity, while terrain characteristics significantly influenced some guilds. The evaluated variables generally had similar effects on guild diversity in both restored and surrounding areas, except for the standard deviation of vegetation height, the effects of which notably differed, particularly on understory nesters and foragers. This study underscores the need to design a mosaic of habitats with complex vertical structures, emphasising the critical role of senescent vegetation and unaltered terrain features in supporting biodiversity. Finally, it provides evidence that integrating habitat heterogeneity metrics derived from airborne remote sensing data into restoration success assessment, can support biodiversity-promoting management interventions.

Keywords:

birds, hyperspectral, lidar, mining, PSRI, spoil heap, structure, terrain

Introduction

Coal mining has long served as the backbone of economic development (Betz et al. 2015; Ericsson & Löf 2019). However, mining in general, and coal mining in particular, also have direct impacts on nature. Especially in open-pit mining, the formation of large pits and the deposition of the excavated material on spoil heaps lead to the destruction of original habitats and biodiversity losses (Aska et al. 2024; Sonter et al. 2018). As a result, tremendous efforts are then made to restore degraded, damaged, or destroyed ecosystems to minimise the environmental impact of mining (Brock 2023; Clewell & Aronson 2013; Martins et al. 2020).

Restoration approaches predetermining the future character of emerging ecosystems are highly debated in relation to biodiversity conservation. Restored sites after coal mining are increasingly recognized for their ecological value to various groups of organisms, including invertebrate and vertebrate species (e.g., Šálek 2012; Harabiš 2023). Habitat heterogeneity (i.e. the variability of environmental conditions such as species dominance and composition, topographic variability, vegetation structure or soil types) is one of the important factors promoting high species diversity. According to the habitat heterogeneity hypothesis, environments with greater variability provide more niches, supporting a higher number of species (see reviews by Stein et al. 2014; Tews et al. 2004). Therefore, habitat heterogeneity is central to ecosystem restoration, and explicit manipulations of habitat heterogeneity—such as targeting specific terrain and vegetation structure parameters in restored ecosystems—can help achieve restoration goals (LaRue et al. 2023; Lengyel et al. 2020; Hendrychová et al. 2020).

For successful restoration, it is crucial to understand the habitat requirements of target species (or groups of species); otherwise, even well-intentioned restoration efforts may fail to benefit wildlife (Poskočilová et al. 2024). Additionally, having detailed and continuous data that accurately represent habitats in the respective area is essential. Although direct field survey of habitat attributes can provide valuable insights into habitat heterogeneity and its importance to various groups of species (e.g., Harabiš et al. 2013; Kolar et al. 2021; Poláková et al. 2022; Delheimer et al. 2023), it is challenging due to its labour-intensive nature and is, therefore, limited both temporally and spatially. Rough subjective estimates of vegetation cover or terrain character, represented by discontinuous, categorical, measures acquired during fieldwork (e.g. Doležalová et al. 2012; Vojar et al. 2016; Kolář et al. 2017; Bellamy et al. 2022), have limited informative value and do not

allow continuous measurement at the comprehensive detail that is much needed for restoration management.

In contrast, remote sensing provides an efficient and cost-effective alternative for such surveys; it, however, remains underutilised in mining restoration studies (Karan et al. 2016; Moudrý et al. 2021; McKenna et al. 2020, 2023). Remote sensing surveys offer an ideal technology to develop indicators relevant to the scale of decision-making, and effective management of restored sites that will maintain high biodiversity. Indeed, hyperspectral and light detection and ranging (lidar) data have revolutionised the measurement of habitat heterogeneity and have been widely used to assess species diversity (LaRue et al. 2023; Moudrý et al. 2023; Cosgrove et al. 2024).The integration of hyperspectral and lidar data supports the characterisation of multiple aspects of species' habitats such as vegetation structure, landcover, terrain, as well as vegetation health and composition (e.g. Melin et al. 2019; Cooper et al. 2020; Prošek et al. 2020; Acebes et al. 2021). Many of these studies have focused particularly (or exclusively) on birds due to the ease of bird data availability and strong relationship of birds with the 3D environment structure (see review by Bakx et al. 2019). While such studies are well-documented in spatially complex ecosystems such as forests (Wallis et al. 2016; Tew et al. 2022; McNeil et al. 2023; Renner et al. 2024), research is comparatively limited in agricultural landscapes (Anderle et al. 2023), urban areas (Choi et al. 2021), and early successional habitats resulting from natural disturbances, (Kebrle et al. 2022), human disturbances (Singh et al. 2017) or in restored sites (Moudrý et al. 2021).

This study aims to assess the applicability of habitat heterogeneity metrics for understanding habitat-bird relationships within the restored areas and their surroundings. By analysing datasets from both early successional habitats (on the restored site) and more typical cultural landscapes, such as managed forests and agricultural areas (surrounding the restored site), this research seeks to provide insights into how bird communities respond to habitat heterogeneity in both early successional and conventional cultural habitats. Specifically, we (**i**) analysed differences in habitat heterogeneity between the restored and surrounding areas of a recently restored mining site to (**ii**) identify the key aspects of habitat heterogeneity most relevant for birds with different nesting, foraging, and diet preferences (i.e. 'guilds'). Besides, we (**iii**) investigated whether there are significant differences in the outcomes of (**ii**) between restored and surrounding areas. Understanding the importance of individual variables and predictability for different avian guilds can aid in restoration planning and management, allowing restoration efforts to be targeted to specific guilds.

Materials and Methods

Study area

The study was carried out on the Radovesická spoil heap and its surrounding area, located in the Northern Bohemian lignite basin in Czechia (Fig. 1). The region is one of the largest active brown coal-mining districts in Europe. From 1964 to 2003, the site served as a deposition of overburden soils from a nearby surface mine. Since 1989, the spoil heap (15.5 km^2; hereafter referred to as 'reclaimed area') has undergone technical reclamation, including terrain modifications, and agricultural and forestry restoration. In addition, 19% of the spoil heap were left to spontaneous succession. The surrounding area (hereafter referred to as 'undisturbed area') includes agricultural fields and mixed forests.

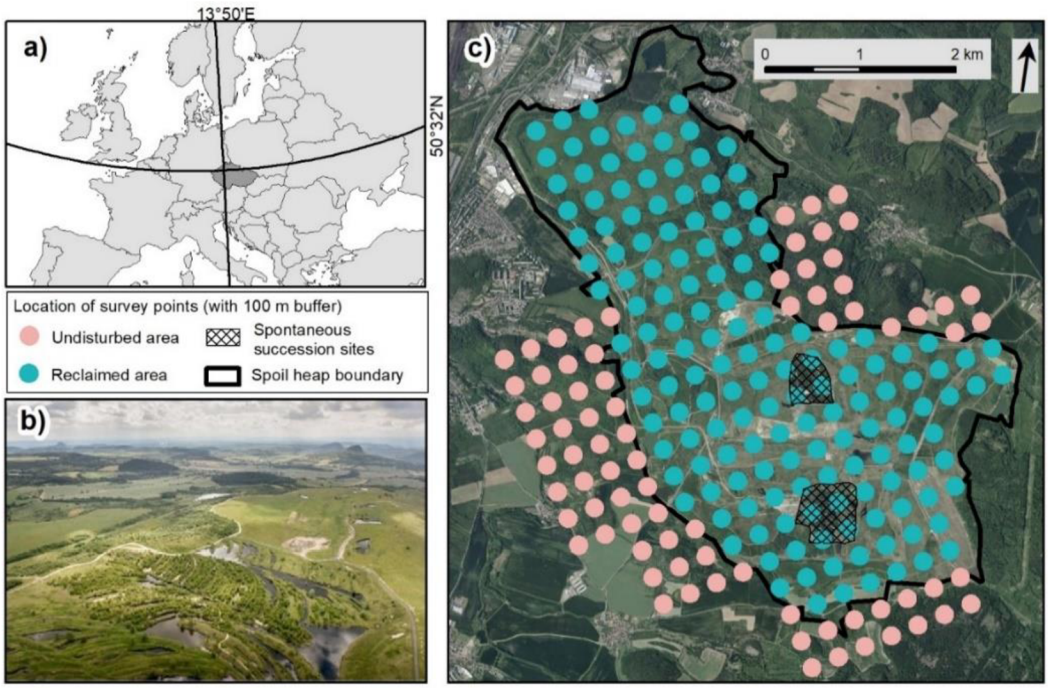

Fig. 1. Study site location and description. a) Location of the study area within Czechia; b) Aerial photo of the study area taken in 2020 (photo by Marketa Hendrychova). Note the area left to spontaneous succession in the bottom part of the image; c) Location of survey points on the actual spoil heap (reclaimed area; blue) and in its surroundings (undisturbed area; pink).

Bird surveys and richness calculations

Birds, due to their dispersal ability, play a critical role in the colonisation of restored sites. Indeed, they are often among the first groups to populate them (Bejček & Šťastný 1984; Cardoso da Silva & Vickery 2002; Martins et al. 2020). Following this premise, we focused our study on bird species. Bird data were collected in May 2012 by five experienced ornithologists, co-authors of this study. Each of the 231 survey points (Fig. 1; 153 on reclaimed and 78 on undisturbed area) were visited twice during the season to increase the likelihood of detecting the pool of existing breeding bird species. The survey points were drawn from a grid spaced at 300 m intervals. At each survey point, all bird individuals identified by sight or sound within a 100 m distance from the survey point were recorded. Following Šálek et al. (2010), we distinguished functional life-history guilds (i.e. groups of species that exploit similar environmental resources in comparable ways; Root (1967)) according to bird's nesting (i.e. ground, understorey, and canopy nesters), foraging (i.e. ground, understorey, and canopy foragers), and diet (carnivores, granivores, omnivores) preferences. Note that species may fall into more than one group (e.g. species can forage on the ground and understorey). The point counts from both visits were pooled together. Individuals recorded beyond the defined distance or while flying over the site were removed. The overall and guild-specific species richness was calculated for each survey point as the number of individual bird species detected (Fig. 2).

Airborne data collection and preprocessing

The airborne hyperspectral (sensor CASI-1500) and lidar (sensor Riegl LMS Q-780) data were acquired using a remote sensing platform FLIS (The Flying Laboratory of Imaging Spectroscopy; Hanuš et al. 2016). Flights were conducted on 18th of May 2017 at an altitude of 1030 m above ground and at a velocity of 110 knots (ground speed).

The hyperspectral imagery contained 48 spectral bands. These covered the visible near-infrared range, from 380 to 1050 nm, with a bandwidth of 7.2 nm. Pre-processing of the hyperspectral images, including radiometric correction, georeferencing, and atmospheric corrections, was carried out by the data provider (CzechGlobe). The average point density of the lidar point cloud data was 8 points per m^2. The data was processed following Moudrý et al. (2021) and georeferenced to the local Datum of Uniform Trigonometric Cadastral Network (EPSG: 5514) and Baltic Vertical Datum – After Adjustment (EPSG: 5705). Following preprocessing, the point cloud was classified into 'ground' and 'vegetation' classes

using LAStools, and ground points were used to derive a digital terrain model (DTM) with a 1 m resolution. In addition, prior to the calculation of vegetation metrics (see Section 2.4), the point cloud was height-normalised (i.e. the returns' height above DTM was calculated).

Habitat heterogeneity (vegetation, terrain) variables

We used six variables describing habitat heterogeneity with potential relevance to bird diversity; four were related to vegetation characteristics and two to terrain structure (Table 1; Fig. 2). For characterising the local vegetation structure, we focused on variables distinguishing individual vegetation layers (i.e. strata). Authors typically recognize two or three layers of vegetation (Lesak et al. 2011; Jones et al. 2013; Vogeler et al. 2014). Here, we distinguished between the understorey layer (1-3m), and the canopy layer (>3m). The height intervals of vegetation layers are based on our field experience. The same vegetation layers are typically recognized during field surveys on postmining sites (e.g. Šálek 2012). We calculated the cover of vegetation layers by counting the number of returns in each layer and dividing it by the total number of vegetation returns (Moudrý et al. 2023). In addition, we calculated the standard deviation of point returns to capture the vertical variability in vegetation structure (e.g. Goetz et al. 2010; Vogeler et al. 2014). We also considered other common vegetation structure variables (i.e. maximum and mean canopy height), but they were highly correlated with the cover of the canopy layer (Pearson's $|r| \geq 0.70$).

Previous research has highlighted the usability of the foliage water content or vegetation senescence as a metric of the habitat suitability for birds (Jones et al. 2013; Soto et al. 2017; Moudrý et al. 2021). Therefore, we calculated the Plant Senescence Reflectance Index (PSRI; $(R_{678} - R_{500})/R_{750}$), which is sensitive to the carotenoid/chlorophyll ratio and, therefore, can serve as an estimate of the amount of old, dead vegetation (i.e. a measure of the vegetation senescence; Merzylak et al 1999). The old, dead vegetation from the previous season is mainly present in aquatic vegetation (e.g. *Phragmites australis* and *Typha latifolia*) and, to a lesser extent, in low-steppe vegetation (e.g. *Calamagrostis epigejos* and *Arrhenatherum elatius*).

In addition, variables characterising the complexity of the terrain have been shown to be particularly important for ground and understorey species (Vogeler et al. 2014; Toivonen et al. 2023). Therefore, to characterise terrain heterogeneity, we calculated the following terrain variables from the DTM: curvature (rate of slope change over the surface), topographic wetness index (TWI), and slope (rate of

elevational change over the horizontal surface), which have been previously used to predict bird occurrences (Besnard et al. 2013, Reif et al. 2018; Hoefs et al. 2021; Anderle et al. 2023). However, the slope was highly negatively correlated with TWI (Pearson's $|r| \geq 0.70$) and it was, therefore, removed from the subsequent analysis.

The terrain variables were aggregated using mean value within the 100 m buffer (Moudrý et al. 2019). We used LAStools (version 200112), ENVI (version 5.5), and ArcGIS (version 10.3) to calculate vegetation structure, senescence and terrain variables, respectively. All metrics were calculated in 100 m surroundings of grid survey points.

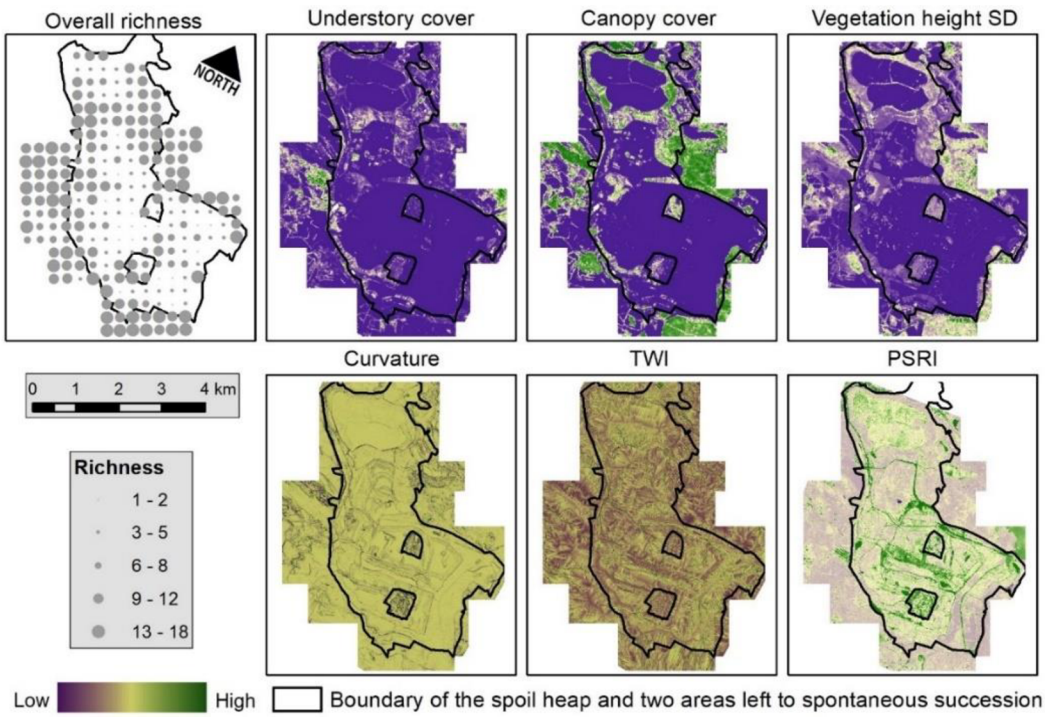

Fig. 2. Bird species richness and explanatory variables. Depiction of the overall bird species richness and six explanatory variables derived from lidar and hyperspectral data that were used for modelling. TWI: Topographic Wetness Index; PSRI: Plant Senescence Reflectance Index. SD: Standard deviation.

Table 1. Overview of explanatory variables. Variables derived using lidar and hyperspectral data. Note that the variables were derived within a 100-m buffer of the survey points.

Variable	Description
Vegetation height SD	Standard deviation of vegetation returns from heights > 1 m
Understorey cover	Number of points between 1 m and 3 m divided by the total number of all points
Canopy cover	Number of points > 3 m divided by the total number of all points
Plant senescence reflectance index (PSRI)	$(R_{678} - R_{500})/R_{750}$ where Rx denotes the reflectance at the wavelength of x nm. Water bodies were excluded from its calculation. The value of this index ranges from -1 to 1. An increase in this index indicates the onset of canopy senescence. The common range for green vegetation is -0.1 to 0.2.
Curvature	Curvature values for a moderate relief typically vary from -0.5 to 0.5. Positive values indicate ridges, while negative values indicate depressions. Near-zero values indicate relatively flat areas or slopes.
Topographic wetness index (TWI)	$TWI = \ln(\alpha/\tan \beta)$, where α is the specific catchment area and β is the local slope in radians. TWI is a surrogate for soil moisture, with low values (<5) on steep slopes where water drains quickly and high values (>10) indicating high moisture in flatter areas or valleys with large contributing areas.

Statistical analyses

We assessed the effect of vegetation and terrain characteristics on bird species richness in undisturbed and reclaimed areas using generalised additive models (GAMs), which allowed for non-linear relationships. We used the Poisson distribution family with a log link function, which was justified by the fact that no over-dispersion was identified in model diagnostics (the maximum dispersion parameter was 0.99). We used thin plate regression spline smoothers with the basis dimension set to 10. The smoothing parameters were estimated by the Generalized Cross Validation criterion (Wood 2017).

We fitted 10 separate models, each having the same predictors (Table 1) but differing in the response variable. The response variable was the species richness of one of the following groups of species (guilds): all species, three nesting guilds (i.e., canopy, understorey, and ground nesters), three foraging guilds (i.e., canopy, understorey, and ground foragers), and three diet guilds (i.e., granivores, carnivores, and omnivores). Additionally, a two-level factor indicating whether a survey point was in the undisturbed or reclaimed area (hereafter reclamation status) was used, both as a main-effect predictor and as interacting with all other predictors.

With each model, we performed a stepwise backward model selection based on AIC. We then recorded the residual autocorrelation (i.e., by computing Moran's correlograms) and overdispersion of the final model. Although in some models we found a significant residual autocorrelation, its actual magnitude was negligible (the maximum of the residual Moran's I for the first distance class of ~500 m was 0.1; the correlograms are in the Fig S1 in the Supplementary material). We evaluated the goodness of fit of each model based on the proportion of the null deviance explained by the model. The effect of each significant predictor ($p < 0.05$) was assessed by plotting a model prediction across the range of the observed predictor values, together with the associated confidence bands.

To compare the relative importance of vegetation characteristics, terrain characteristics, and reclamation on the bird species richness, we performed variation (deviance) partitioning (Ozdemir 2015). This technique consists in comparing the deviance explained by the models with and without the given group of predictors and includes an estimate of parts of deviance which cannot be solely attributed to one of the predictor groups due to its collinearity with other group(s). The resulting fractions of the deviance explained by the individual groups, as well as that shared by multiple groups (due to the collinearity among them), were then visualised using Venn diagrams.

All statistical analyses were performed in R 4.3.1 (R Core Team 2023). We used the *mgcv* package for GAM modelling (Wood 2017), the *pgirmess* package for computing correlograms (Giraudoux 2023), and the *tidyverse* meta-package to process data and to produce graphics (Wickham et al. 2019).

Results

Habitat heterogeneity on reclaimed and undisturbed areas

Comparison of the heterogeneity of the 231 survey points, with 153 in the reclaimed area and 78 in the undisturbed area, showed the following differences. The reclaimed area was characterised by low canopy and understory cover, and a relatively low standard deviation of vegetation height. In contrast, the undisturbed area had higher understory and canopy cover, as well as a higher standard deviation of vegetation height. In terms of terrain characteristics, curvature was similar in both areas, while the TWI was higher in the reclaimed area. Similarly, the PSRI was considerably higher in the reclaimed area (Fig. 3).

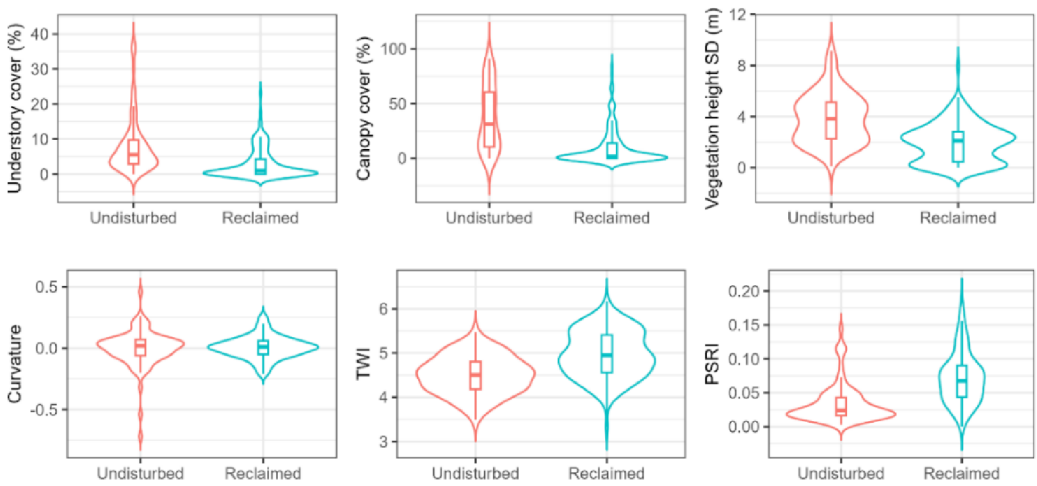

Fig. 3. Habitat heterogeneity. Violin plots showing the differences in habitat heterogeneity variables between reclaimed and undisturbed areas. TWI: Topographic Wetness Index; PSRI: Plant Senescence Reflectance Index. SD: Standard deviation.

Overall richness

We observed 83 bird species from a total of 1,340 individual bird records. The overall bird species richness ranged from 1 to 17 and 1 to 18 species per survey point in reclaimed and undisturbed areas, respectively. The median species richness in the reclaimed area was 6, and it was dominated by carnivorous ground-foraging and ground-nesting birds (Fig. 4-5). The median species richness in the undisturbed area was 12, and was dominated by carnivorous understory- and canopy-nesters (Fig. 4-5).

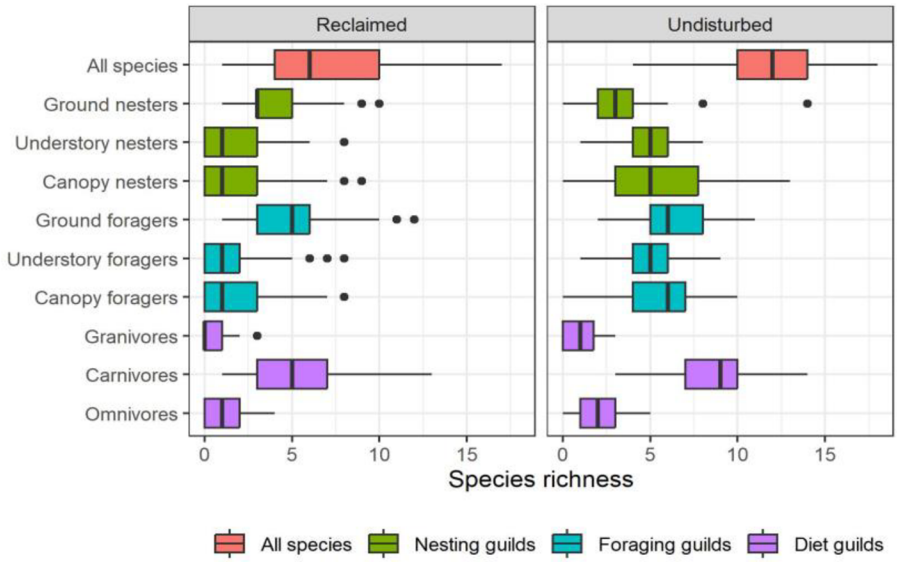

Fig. 4. Species richness. Differences in species richness of nine guilds between reclaimed and undisturbed areas

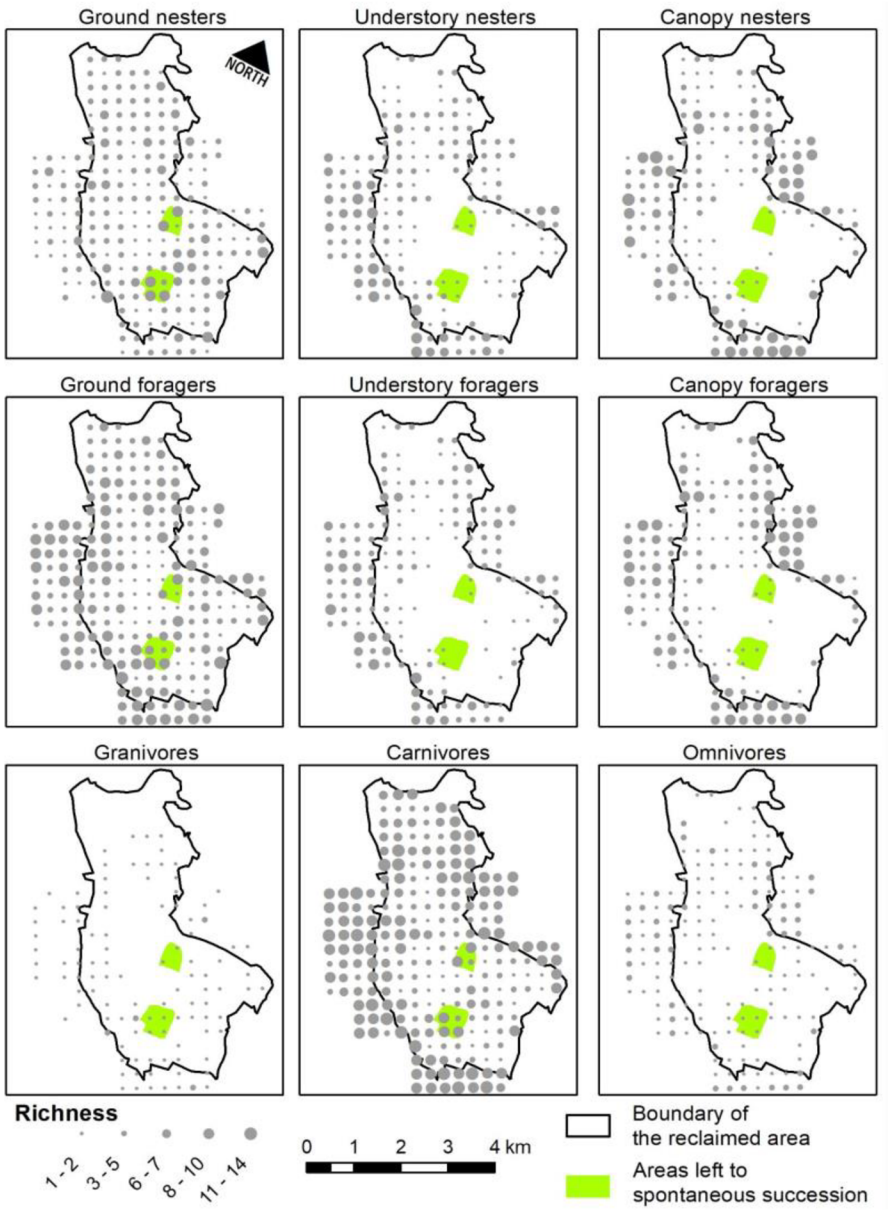

Fig. 5. Species richness per guild. Spatial distribution of richness of individual guilds on the reclaimed site and the surrounding undisturbed area. Note the two sites left to spontaneous succession without reclamation.

The GAM model of overall species richness explained 70.6% of deviance (coefficients of all models are reported in Tabs S1 and S2 in the Supplementary materials). Overall species richness was strongly affected by vegetation characteristics (i.e., vegetation senescence and structure), while the reclamation status (i.e., reclaimed vs. undisturbed area) showed a moderate effect, and terrain characteristics a weak effect (Fig. 6a). Notably, 23.6% of the variability explained by vegetation characteristics overlapped with the variability explained by the reclamation status (Fig. 6a), indicating that these factors are interrelated. Response

curves showed that both vegetation characteristics and the reclamation status significantly influence species richness. The shape of observed response curves were similar for both the reclaimed and the surrounding undisturbed area, except for understorey cover (Fig. 6b). Standard deviation of height and presence of senescent vegetation (PSRI) had a strong positive effect and resulted in a gradual increase in overall species richness (Fig. 6b). Species richness increased considerably at relatively low values of canopy cover and understorey cover (only in the reclaimed area), with minimal change as these variables continued to increase. The values where the changes took place for the canopy density and understorey density were 0 – 25% and 0 – 5%, respectively (Fig. 6b).

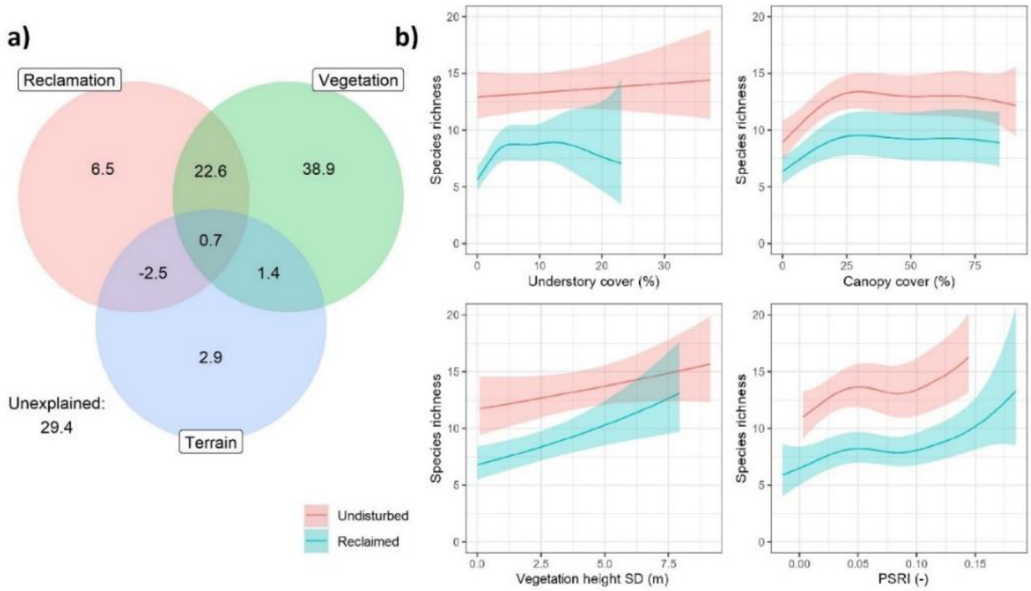

Fig. 6. a) Venn diagram showing the percentage of explained (and unexplained) deviance in bird species richness explained by the three groups of predictors: vegetation characteristics (understorey cover, canopy cover, standard deviation of vegetation height, PSRI), reclamation status (reclaimed vs. undisturbed area), and terrain characteristics (curvature, topographic wetness index). The overlap of the circles indicates fractions of the variation that cannot be unequivocally attributed to only one of the overlapping predictors. For example, when vegetation characteristics differ also between reclaimed and undisturbed sites, a fraction of the explained deviance will be shared between them. Negative numbers can arise due to the spline optimisation algorithm during model fitting; these are, however, usually small and can be interpreted as zeroes. b) Response curves derived from generalised additive models, showing the relationships between the overall bird species richness and the evaluated habitat heterogeneity variables (only significant variables presented) and the differences between reclaimed and undisturbed areas. The shaded areas represent the 95% confidence bands.

Nesting guilds

GAM models explained 71% and 70% of the variability in the richness of canopy and understorey nesters, respectively (Fig. 7a). The richness of canopy and understorey nesters was strongly affected by vegetation characteristics, with reclamation status having a moderate effect that shared a large portion of the explained variability with vegetation characteristics. The terrain characteristics had a weak effect (Fig. 7a). The richness of canopy nesters increased with increasing canopy density. Increasing standard deviation of vegetation height positively affected canopy nesters on the spoil heap but showed more complex relationship in the surrounding undisturbed area. Richness decreased for standard deviation of vegetation height between 0 and 2.5, then increased for higher values (Fig. 8). The richness of understorey nesters increased with increasing understorey density and standard deviation of height returns (in the reclaimed area only) and decreased with increasing canopy cover. Increasing terrain curvature negatively affected both canopy and understory nesters. For the ground nesting guild, GAM models explained 36% of the variability in its richness, and the ground nesting guild was equally affected by vegetation and terrain characteristics (Fig. 7a). The richness of ground nesters was positively affected especially by PSRI and TWI (only on undisturbed area), and, to some degree, by canopy cover (Fig. 8).

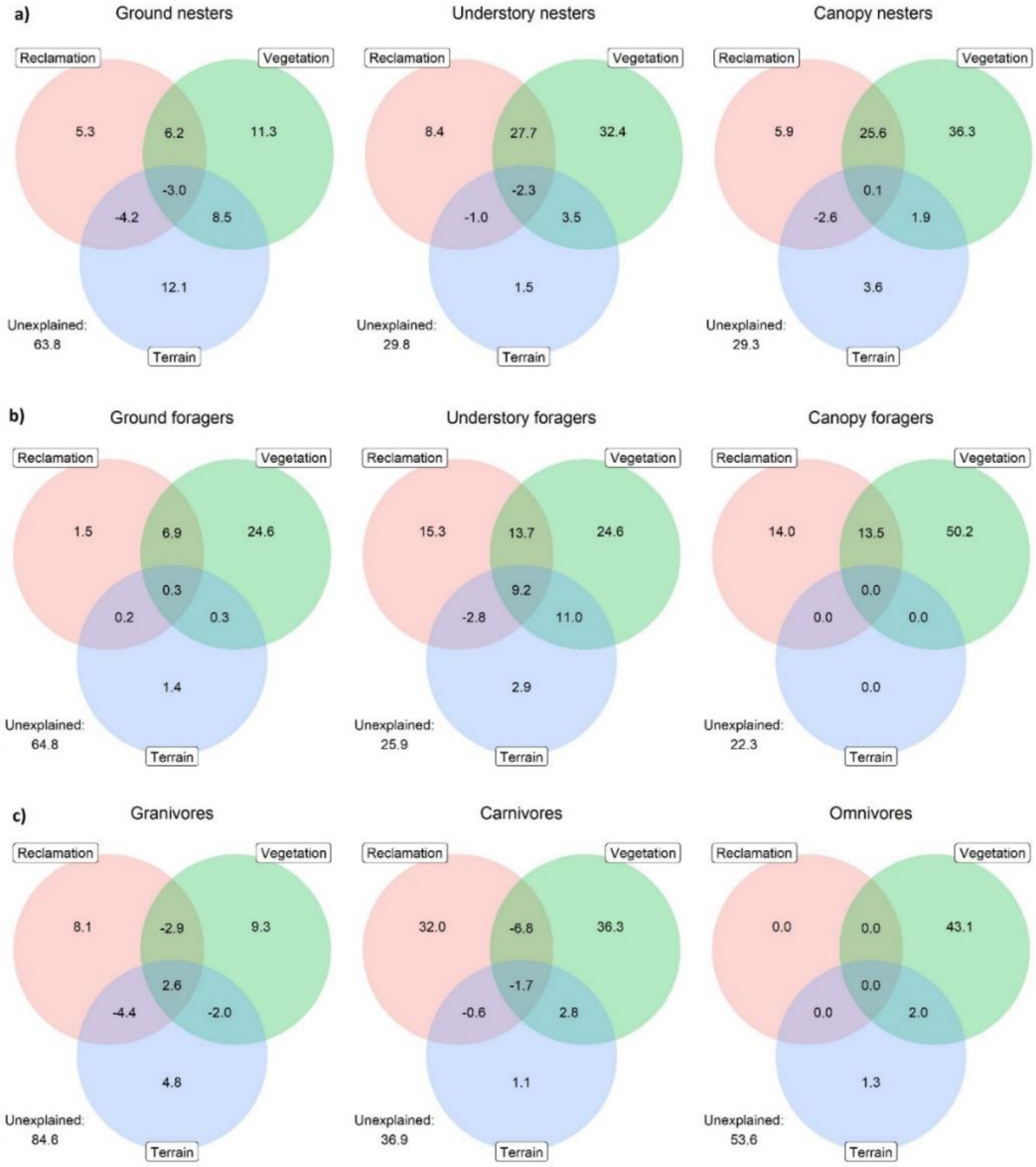

Fig. 7. Venn diagrams showing the percentage of explained (and unexplained) deviance in the richness of a) nesting, b) foraging, and c) diet guilds, as explained by the three groups of predictors: vegetation characteristics (understorey cover, canopy cover, standard deviation of vegetation height, PSRI), reclamation status (reclaimed vs. undisturbed area), and terrain characteristics (curvature, topographic wetness index). The overlap of the circles indicates fractions of the variation that cannot be unequivocally attributed to one of the overlapping predictors.

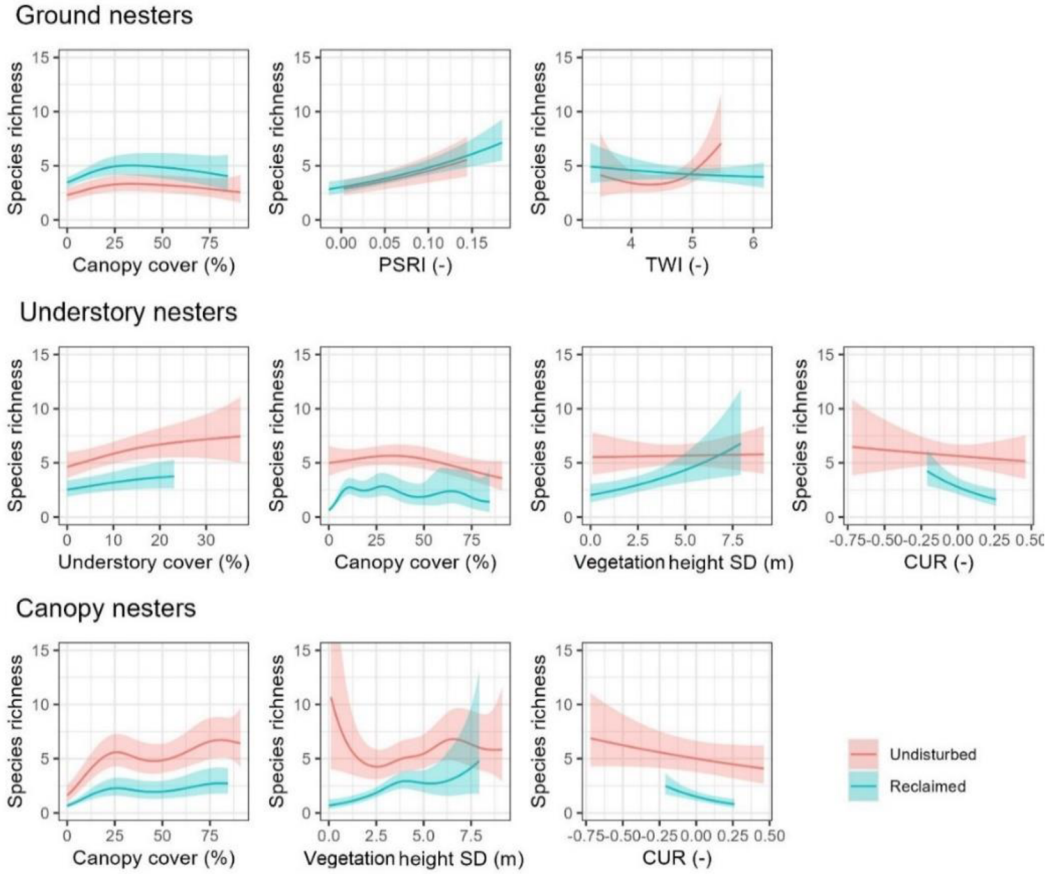

Fig. 8. Response curves derived from generalised additive models, showing the relationship between the nesting guilds richness (ground, understory, and canopy nesters) and the evaluated habitat heterogeneity variables (only the significant variables are shown) and the differences between reclaimed and undisturbed areas. TWI: Topographic Wetness Index; PSRI: Plant Senescence Reflectance Index. CUR:Curvature, SD: Standard deviation.

Foraging guilds

GAM models explained 77%, 74% and 35% of the variability in the richness of canopy foragers, understory foragers, and ground foragers, respectively (Fig. 7b). The richness of all foraging guilds was strongly affected by vegetation characteristics, with the reclamation status having a moderate effect that shared a considerable portion of the explained variability with vegetation characteristics. The terrain characteristics had a weak effect (Fig. 7b). The richness of canopy foragers increased with increasing canopy cover and the standard deviation of height returns. The richness of ground and understory foragers increased with canopy cover up to 20-25% and then gradually decreased. Increasing standard deviation of vegetation height and, to some degree, the understory cover positively affected understory foragers in the reclaimed area but showed no effect in the

surrounding undisturbed area (Fig. 9). Their richness also tended to decrease with terrain curvature but only in the reclaimed area.

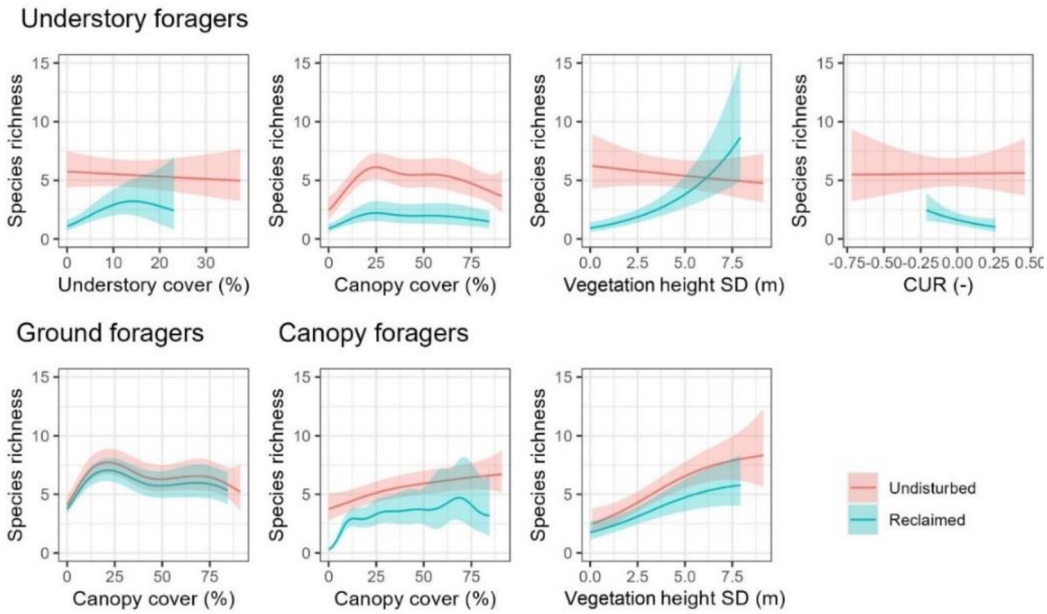

Fig. 9. Response curves derived from generalised additive models, showing the relationship between the foraging guilds richness (ground, understory, and canopy foragers) and the evaluated habitat heterogeneity variables (only significant variables presented) and the distinction between reclaimed and undisturbed areas. TWI: Topographic Wetness Index; PSRI: Plant Senescence Reflectance Index. CUR:Curvature, SD: Standard deviation.

Diet guilds

GAM models explained 15%, 63% and 46% of the variability in richness of granivores, carnivores, and omnivores, respectively (Fig. 7c). The richness of all diet guilds was affected by vegetation characteristics and reclamation status, while terrain characteristics had a negligible effect (Fig. 7c). The observed patterns were relatively similar for both the reclaimed and the surrounding undisturbed area, except for a few exceptions mentioned below. The richness of carnivores increased with canopy cover, up to 25% in reclaimed areas and 50% in undisturbed areas, respectively. PSRI also positively affected the richness. Decreasing curvature and standard deviation of height returns positively affected carnivores in the reclaimed area but showed no effect in the undisturbed area (Fig. 10). TWI was the only variable that significantly affected granivores but its effect on their richness was negligible. The richness of omnivores increased with the increasing standard deviation of height returns, understory and canopy cover.

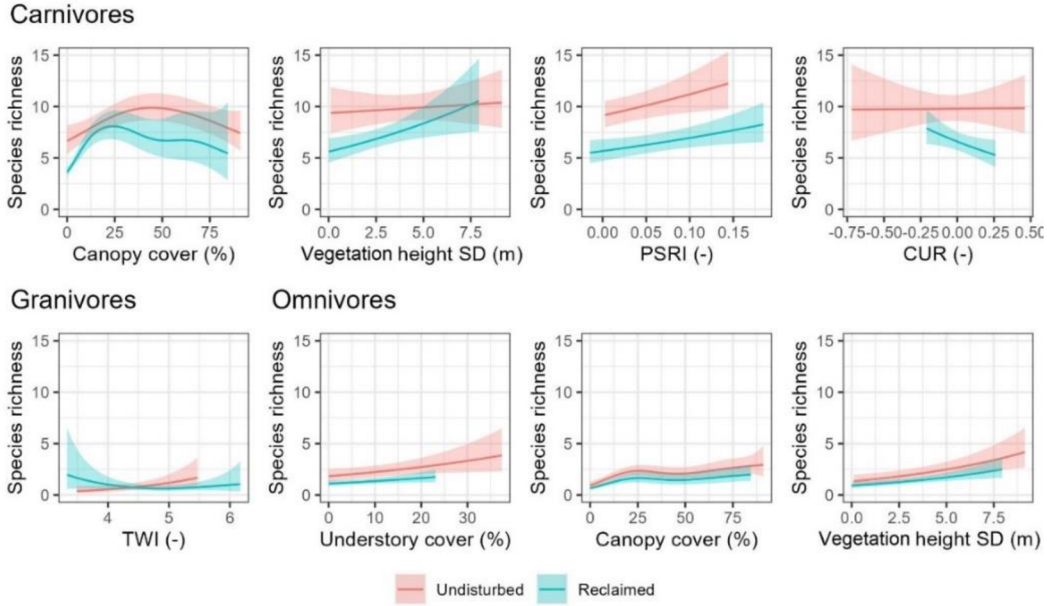

Fig. 10. Response curves derived from generalised additive models, showing the relationship between the diet guilds richness (carnivores, granivores, and omnivores) and the evaluated habitat heterogeneity variables (only the significant variables are shown) and the difference between reclaimed and undisturbed areas. TWI: Topographic Wetness Index; PSRI: Plant Senescence Reflectance Index. CUR:Curvature, SD: Standard deviation.

Discussion

In this study, we evaluated the effect of habitat heterogeneity derived from airborne lidar and hyperspectral data, on the overall and guild-specific bird species richness, both within a restored coal-mining site and in its vicinity. While the reclaimed area was dominated by ground-nesting and ground-foraging birds, the undisturbed area was dominated by the understory and canopy nesters (Fig. 4-5). Our results show a significant effect of vegetation and terrain characteristics on the richness of individual guilds. Models of overall and guild-specific bird species richness demonstrated relatively good performance, with seven out of ten models explaining more than 40% of the variability in bird species richness.

Explained variability

Models of canopy and understory nesters and foragers explained between 70–77 % of the variability in their richness. In contrast, models of ground nesters and

foragers explained considerably less variability (approximately 35%). Models of diet guilds explained between 15%–63% of the variability, with carnivores showing the best model performance and granivores the worst. The explained variabilities are slightly higher than those reported by prior studies that also explored the relationship between habitat heterogeneity (derived from lidar and passive remote sensing data) and various guild-specific bird species richness. For example, Goetz et al. (2007) and Jones et al. (2013) distinguished avian guilds according to habitat preferences, with their models explaining 30%–48% and 20%–65% of variability, respectively. Voegler et al. (2014) focused on nesting guilds, and their models explained 5%–42% of the variability. Similarly, Lesak et al. (2011) categorised guilds based on nesting and foraging behaviours, with their models accounting for 15%–20% of the variation in guild richness.

Importance of individual variables

Overall richness was strongly affected by understory and canopy covers, as well as by the standard deviation of height, and PSRI (Fig. 6b). Canopy and understory nesters and foragers showed a positive response to vegetation characteristics. In contrast, ground nesters were influenced by factors related to senescence and terrain (Fig. 8-9). Finally, different diet guilds responded to various factors: omnivores were affected by the vegetation structure, granivores by the terrain, and carnivores by the vegetation structure, terrain, and senescence (Fig. 10). This aligns with previous studies that have shown scrub and forest species are relatively easy to model using lidar-derived vegetation structure (e.g., Goetz et al. 2007). In contrast, ground-nesting and foraging species are typically less accurately predicted by vegetation structure alone (e.g. Lesak et al. 2011; Weisberg et al. 2014), with water content (i.e., senescence) in surface vegetation often serving as a more important explanatory factor for their richness (e.g., Jones et al. 2013; Cooper et al. 2020).

Canopy cover had a positive effect, especially on the richness of canopy nesters and foragers. The diversity of ground and understory nesters and foragers increased with canopy cover to approximately 25%, but high values led to a decline in their richness. Understory cover had a positive effect on the richness of understory nesters and, to some extent, on understory foragers and omnivores. Curvature affected the richness of canopy and understory nesters, understory foragers, and carnivores, with richness increasing as curvature decreased. TWI was important for granivores and ground nesters, particularly in the undisturbed area, where their richness increased with higher TWI. Similarly, PSRI (i.e. senescent

vegetation), was significant for the richness of ground nesters and carnivores. The importance of both TWI and PSRI might be explained by similar reasons. Areas with higher moisture and a greater density of senescent vegetation offer more food resources and nesting sites. Reduced predation risk could be another potential factor, though this was not confirmed (Novak & Hendrychova 2021). Such conditions are typical for areas left to spontaneous succession (Fig. 1c), a valuable areas known for its positive impact on the diversity of multiple taxa (Šálek 2012; Řehounková et al. 2018), which are characterised by specific rugged terrain resulting from the heaping of overburden material, early successional stages of vegetation (Fig. 1b), and old dead aquatic vegetation such as *Phragmites australis* and *Typha latifolia* from the previous vegetation season (see Fig. 2 for high PSRI values on these sites). See Fig. 5 for the richness of ground nesters and carnivores in these areas.

Reclaimed versus undisturbed area

The comparison between the reclaimed and undisturbed areas showed considerable differences in habitat heterogeneity (Fig. 3). This explains why the variability explained by vegetation characteristics often overlaps with the variability explained by the predictor distinguishing reclaimed areas from the undisturbed ones (Fig. 6a-7), indicating that these factors are interrelated. The evaluated variables had in general the same effect (i.e., the shapes of the response curves were relatively similar) on the diversity of individual guilds both on the reclaimed and undisturbed area (Fig. 8-10), suggesting that the adopted variables can be used as universal metrics suitable for habitat assessment in reclaimed as well as surrounding landscapes. The standard deviation of vegetation height was the most striking exception, showing some differences in effects between the reclaimed and undisturbed area. It is therefore important to use such habitat heterogeneity metrics with caution. Understory nesters and foragers were positively associated with increasing standard deviation of vegetation height in the reclaimed area, but no or slightly negative effect was observed in the undisturbed area. For example, Heidrich et al. (2023) also used the standard deviation of vegetation height as a measure of vertical heterogeneity and found an increase in bird diversity with increasing vertical heterogeneity. The contrasting results in our study are due to the fact that relatively high values of the standard deviation of vegetation height can be associated with both low vegetation in the reclaimed area and tall vegetation in the undisturbed area (Fig. 2). In undisturbed areas, the combination of a high standard deviation in vegetation height and canopy cover creates conditions that are less suitable for understory foragers and nesters.

Implications for restoration planning and management

Understanding habitat characteristics that influence species distributions in restored/decommissioned mining areas, as well as monitoring these factors, is crucial to assuring long-term biodiversity benefits. In the EU, such monitoring capabilities will guide the development of national restoration plans, as expected in the scope of the Nature Restoration Law (European Union 2024). In Czechia, in particular, the current phasing-out from coal-based energy production, which is to be completed by 2033, will further benefit from remote-sensing-based biodiversity monitoring capabilities such as those explored in our study. The guidelines provided here will help plan efforts in the restoration of decommissioned coal-mining sites, creating bilateral benefits for the national energy transition and national restoration targets. Although we focused our study on a single site, we developed a standardised, data-driven workflow that can be extended to other mining regions.

Monitoring in restored ecosystems often requires a combination of in-situ field surveys focused on species richness and vegetation characteristics (see reviews by Wortley et al. 2013 and Martins et al. 2020). However, vegetation characteristics alone, particularly vegetation structural diversity derived from remote sensing data, can be used as a rapid and effective measure for assessing restored site conditions and informing management practices (Gibbons & Freudenberger 2006, LaRue et al. 2023). Our study demonstrates that habitat heterogeneity characteristics — such as terrain, vegetation structure, and senescence — derived from remote sensing data offer useful variables that can be used for restoration success (sensu biodiversity support), assessment, and planning. Compared to field surveys, hyperspectral and lidar data offer greater potential for delivering information that can be directly applied to management actions (Jones et al. 2013; Cooper et al. 2020; Moudrý et al. 2021; Anderle et al. 2023; Rigo et al. 2024).

With the continuous increase in remote sensing data availability, its application in restoration ecology is highly promising, particularly for assessing vegetation characteristics (Martins et al. 2020; Szostak et al. 2020). In addition, in areas where multiple acquisitions exist, assessment of the temporal development of vegetation structure and associated species assemblages is possible (Korejs et al. 2023; Paudel et al. 2024). Our results show that habitat heterogeneity represented by vegetation vertical variability (i.e. standard deviation of returns), understory/canopy cover, and vegetation senescence are potentially relevant for such assessments.

Conclusions

Spoil heaps represent valuable early successional habitats that are otherwise disappearing from the human-managed landscape. We demonstrated how vegetation and terrain characteristics of such restored site and its surrounding area influence bird species richness, and how remote-sensing-based, continuous variables on habitat heterogeneity can be used to monitor the restored area. Our findings provide practical recommendations for management strategies that enhance biodiversity conservation on restored sites and their surroundings, while also offering a methodological basis for more extensive monitoring of other mining regions in transition, enabling managers to assess habitat characteristics within a broader landscape.

Acknowledgements

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SUPPLEMENTARY MATERIAL

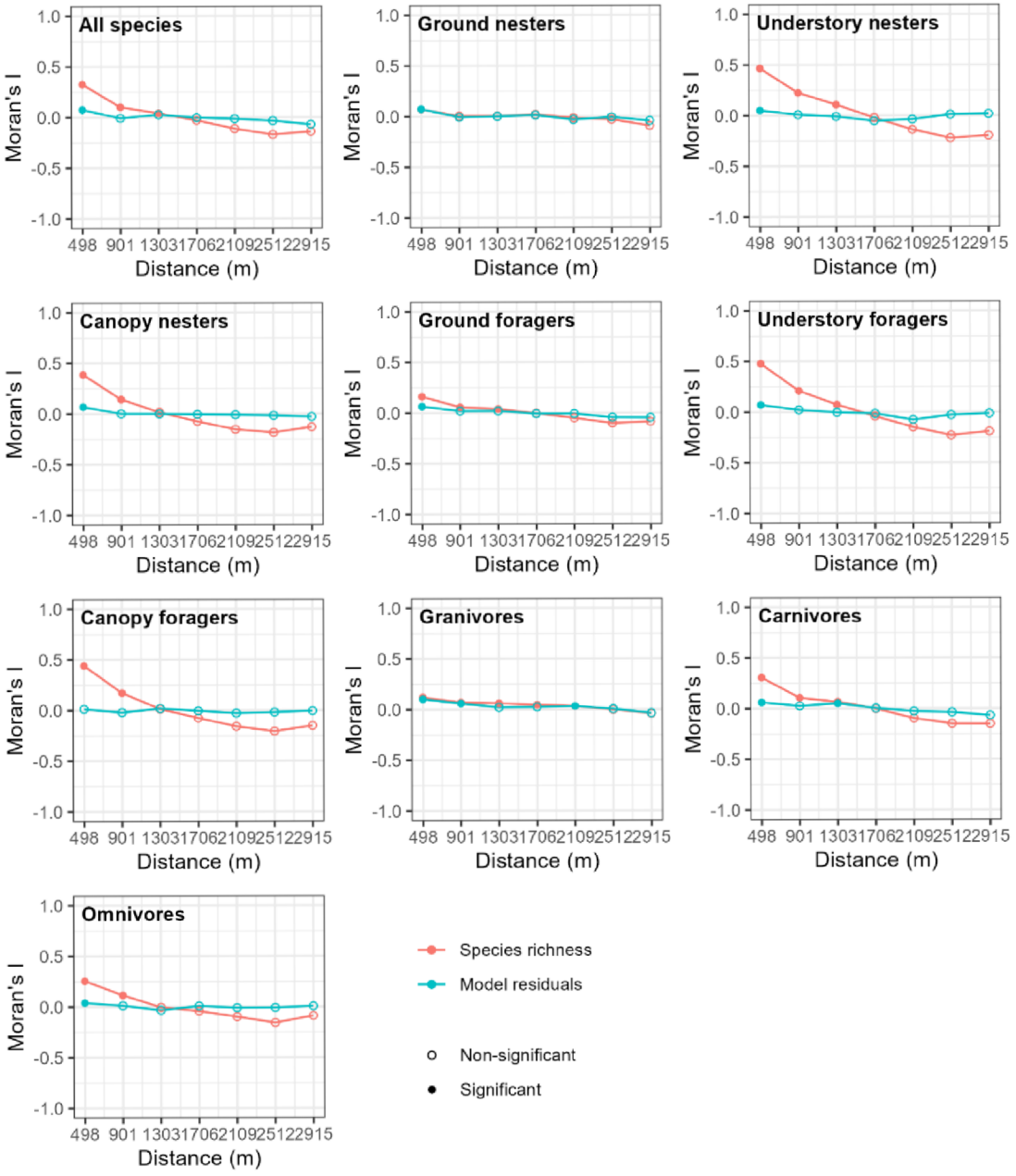

Fig. S1. Correlograms for species richness of each species group as well as for residuals from a corresponding generalized additive model.

Table S1. Table of coefficients of the parametric terms of the GAM models. Individual models are in columns. Parameter estimates ± standard errors are reported, together with the standard identification of significance based on Wald tests.

Term[a]	All species	Ground nesters	Understory nesters	Canopy nesters	Ground foragers	Understory foragers	Canopy foragers	Granivores	Carnivores	Omnivores
Intercept	2.326 ± 0.054 ***	1.019 ± 0.107 ***	1.464 ± 0.08 ***	1.274 ± 0.118 ***	1.644 ± 0.067 ***	1.372 ± 0.088 ***	1.212 ± 0.085 ***	-0.33 ± 0.185	1.958 ± 0.066 ***	-0.264 ± 0.144
RNR	-0.38 ± 0.086 ***	0.005 ± 0.102	-1 ± 0.113 ***	-0.896 ± 0.142 ***	-0.152 ± 0.07 *	-1.167 ± 0.124 ***	-0.934 ± 0.123 ***	-0.423 ± 0.245	-0.388 ± 0.069 ***	-
PSRI	-	4.642 ± 1.022 ***	-	-	1.747 ± 0.894	-	-	-	2.031 ± 0.849 *	-
CUR	-	-	-	-	-0.423 ± 0.242	-	-	-	-	-0.732 ± 0.383
SD	-	-	-	-	-	-	-	-	-	0.126 ± 0.037 ***
UC	-	-	-	-	-	-	-	-	-	0.02 ± 0.009 *

[a] The predictors are coded as follows: UC – Undestory cover, SD – Canopy cover SD, PSRI – PSRI index, CUR – Terrain curvature, TWI – TWI index, RNR – Restoration, level Restored

Table S2. Significance of smooth terms of the GAM models. Individual models are in columns. Effective degrees of freedom (a measure of degree of nonlinearity) together with the χ^2 statistics are reported. The asterisks refer to the approximate significance of the smooth terms (ignoring the uncertainty of the smoothing parameters estimation).

Smooth term[a]	All species	Ground nesters	Understory nesters	Canopy nesters	Ground foragers	Understory foragers	Canopy foragers	Granivores	Carnivores	Omnivores
D:RNN	1(2.16)	-	1(0.02)	4.66(8.68)	-	1(0.65)	-	1.3(1.38)	1(0.21)	-
SD:RNR	1(10.26) **	-	1(8.41) **	3.64(29.91) ***	-	1(30.68) ***	-	2.47 (4.91)	1(6.94) **	-
UC:RNN	1(0.38)	-	-	1(2.05)	-	1(0.26)	-	-	-	-
UC:RNR	3.54(15.47) **	-	-	1(2.08)	-	2.15(17.14) ***	-	-	-	-
CUR:RNN	1(0.32)	-	1(0.29)	1(2.15)	-	1(0)	-	-	1(0)	-
CUR:RNR	4.54(10.09)	-	1(8.12) **	1(12.18) ***	-	1.09(6.45) *	-	-	1 (4.6) *	-
CC	3.37(13.19) *	2.66(11.71) *	-	5.07(37.68) ***	4.83(57.72) ***	4.31(21.67) ***	-	3.07(7.12)	-	4(24.01) ***
PSRI	3.49 (12.79) *	-	1.44 (3.01)	-	-	-	-	-	-	-
TWI:RNN	-	2.13(7.58) *	-	-	-	1(0.03)	-	1(4.77) *	-	-
TWI:RNR	-	1.17(0.88)	-	-	-	4.81(9.3)	-	2.13(4.2)	-	-
CUR	-	6.15(9.64)	-	-	-	-	-	-	-	-
CC:RNN	-	-	1.91(5.12)	-	-	-	2.02(8.81) *	-	2.32(9.91) *	-
CC:RNR	-	-	6.59(48.05) ***	-	-	-	7.13(111.98) ***	-	4.17(57.21) ***	-
UC	-	-	1.57(5.63) *	-	-	-	-	-	-	-
SD	-	-	-	-	-	-	1.99(28.25) ***	-	-	-

[a] The predictors are coded as follows: UC – Undestory cover, CC – Canpy cover, SD – Canopy cover SD, PSRI – PSRI index, CUR – Terrain curvature, TWI – TWI index, RNR – Restoration, level Restored, RNN – Restoration, level Not restored

Chapter VI – Discussion and Summary

The following section of the dissertation presents the overall discussion and summary. Since the discussions and conclusions for the individual research studies in Chapters 3-5 have already been provided within those chapters, this chapter aims to link the individual research studies, explore the most intriguing aspects of this research, provide insight into how the results have been cited and utilized, and suggest potential future directions.

Common bird species in modern settlements

The decline of common species, such as the house sparrow, is often overlooked in favor of focusing on rare species. However, this oversight is problematic given the critical role common species play in the ecosystem functioning and the provision of ecosystem services (Grime 1998; Geider et al. 2001; Gaston 2008, 2011). Although common species may represent a smaller proportion of overall species richness, their contributions to the structure, character, and dynamics of ecosystems are substantial. In this context, even minor proportional declines in their populations can lead to significant losses in the numbers of individuals and in the amount of biomass, which can have cascading ecosystem consequences (Ellison et al. 2005; Gaston 2010).

The inclusion of this broader ecological perspective is crucial to understanding the implications of our study on the house sparrow. House sparrows, despite being a common species, are experiencing population declines in various parts of the world, including Europe, where populations are declining in 15 countries (Jokimäki et al. 2021). This decline is not isolated to sparrows but reflects a larger trend affecting species nesting in buildings (Inger et al. 2015). House sparrows have often been used as a model species to study the impacts of urbanization, and our study has contributed to this discourse. Therefore, the findings from **Study 1** on house sparrows have a wider regarding the decline of common urban bird species that are integral to ecosystem functioning.

Several years after the publication of our **Study 1**, we can now reflect on its contribution to the scientific community and evaluate how it has been used by other researchers (i.e., cited). **Study 1** was published in the highly ranked journal Landscape and Urban Planning and has been relatively often referred to. It was published in 2018 and since, it has been cited 41 times according to Google Scholar, and 23 times according to Web of Science (as of October 2024). Researchers frequently cite our work when discussing house sparrow abundance in built-up areas (e.g. Bernat-Ponce et al. 2018; Angelier & Brischoux 2019; Beaugeard et al. 2021; Havlíček et al. 2021; Bernat-Ponce et al. 2022a; Ishii et al. 2022) and negative effect of modernization on their abundance (Bernat-Ponce et al. 2020; Jokimäki et al. 2021; Liordos et al. 2021; Mohring et al. 2021). Some authors extend our findings to more general topics, such as generalizing our results to the entire group of cavity nesters (e.g., Angelier & Brischoux 2019), or referring to availability prey availability (Beaugeard et al. 2019), which reflects the broader applicability of our research to urban ecological studies.

The decline of house sparrows has been studied across a variety of spatial scales, from broad socio-economic factors at coarse scales (e.g., Bernat-Ponce et al. 2018) to highly localized aspects such as the availability of nesting sites (e.g., Dulisz et al. 2022). In **Study 1**, we highlighted the significance of scale when analyzing anthropogenic pressures on house sparrow populations. Understanding these pressures requires a nuanced approach, as the drivers of decline operate across multiple levels of scale. This was further supported by Strubbe et al. (2020) who concluded that conservation and mitigation measures aiming to reduce the impacts of urbanization on free-ranging populations are most effective when implemented across various spatial scales.

However, in the following discussion, I focus on several fine-scale factors (such as the availability of greenery, food sources, and nesting sites) crucial for maintaining viable urban populations. These fine-scale aspects should be integrated into urban planning strategies to support urban birds' conservation efforts. While larger-scale socio-economic drivers are important, localized interventions, such as the preservation of green spaces and nesting habitats, play a vital role in countering the negative effects of urbanization on bird populations.

Nesting places for House sparrows

The fact that sparrows are less abundant in newly built-up areas compared to old built-up areas in the outskirts of Prague was one of the main findings of **Study 1**. This finding suggests that the modernization of villages may have a dramatic effect

on the abundance of species breeding in or on buildings. The architectural design of modern buildings often lacks the features necessary for bird nesting. New buildings are well-insulated and, as a consequence, the availability of potential nesting sites (hollows and cavities) is reduced compared to old buildings (Rosin et al. 2016). New urban structures without any cracks or cavities may preclude cavity nesters from breeding in cities, which may cause population declines. Similarly, the renovation of old buildings may considerably reduce the number of potential nesting sites for species nesting in buildings (Rosin et al. 2020). Requirements for the improvement of the energy performance of the buildings and people's need for a high standard of living have vastly changed the structure of rural architecture and habitats across the whole European Union (Antrop 2004; Bański & Wesolowska 2010). It is not surprising, then, that many studies investigating the abundance of sparrows in relation to different types/levels of urbanized environments have been performed.

To mitigate the lack of cavities, nest boxes are often proposed as an alternative nesting option. For example, Angelier & Brischoux (2019) showed that rural nest boxes were more likely to be occupied by house sparrow than urban ones, suggesting that the availability of nesting cavities is probably more constraining in rural areas than in urban ones and, in effect, that urban house sparrow populations are probably not constrained by a lack of nesting sites in medium size cities. In a recent study, Dulisz et al. (2022) showed that using nest boxes to compensate for bird nesting sites (including house sparrow) lost during the modernization of buildings can cause a population to recover to approx. 50% of its original level. This is interesting as in **Study 1** we discuss that although nesting site opportunities for house sparrows could be increased by using artificial nesting boxes, such measures have been shown to have no effect on rural house sparrow abundance (von Post & Smith 2015).

Contrary to our findings in **Study 1**, Mohring et al. (2021) reported that the number of house sparrows was not higher at sites covered mainly with old buildings, which are commonly associated with nesting sites, compared to sites with relatively new buildings in Paris. The discrepancy between our findings and theirs may partly be explained by the differences in green space availability in newly developed areas. In our study, newly built-up areas had little to no green space, which likely also contributed to the lower sparrow numbers observed there. On the other hand, Mohring's study reported higher sparrow occurrence in areas of relatively new developments in Paris, which were, however, associated with a relative abundance of greenery. This may have compensated for the lack of traditional nesting sites in newer buildings. Such results highlight the complex

interaction between nesting availability, food resources, and species abundance. In addition, Nath et al. (2022) showed that house sparrows occupied commercial areas and a combination of commercial-residential sectors and avoided areas with a low level of urbanization (city outskirts) in the city of Guwahati in India. All these results imply that local urban conditions, including habitat characteristics and human activities, play an important role in determining where house sparrow populations thrive.

Overall, it is evident that the decline of house sparrows is closely linked to changes in urban architecture, particularly the reduction of natural nesting sites in modern and renovated buildings. While artificial nest boxes can offer some mitigation, their effectiveness varies. Finally, the interplay between nesting availability and other factors, such as food resources and green spaces, plays a critical role in determining house sparrow populations. These ecological factors will be further examined in the following chapter.

Role of food availability and greenery in urban environments for house sparrows

The access to diverse and reliable food sources is critical for the survival and reproductive success of house sparrows in urban environments (Bernat-Ponce et al. 2023). Urban sparrows must adapt to a mosaic of food availability shaped by human activities, green spaces and the built-up environment. They rely on a variety of food sources, from natural seeds and insects found in parks and gardens to anthropogenic options such as discarded human food (Bernat-Ponce et al. 2018). Variations in food availability, influenced by both socio-economic factors and urban layout, directly affect house sparrow populations and their ability to thrive in different parts of the urban landscape.

The availability of food resources can particularly vary between the new and old urban developments. In newly developed areas, which are characterized by higher socioeconomic status and less localized human activity, sparrows face a lack of anthropogenic food sources. Moreover, highly maintained gardens typical for such areas limit insect abundance. In contrast, human activities such as urban agriculture or domestic husbandry are more common in older neighborhoods with more diverse socio-economic conditions; similarly, gardens in such neighborhoods tend to be less intensively managed, offering a richer foraging environment. People in less developed areas are also more willing to sacrifice some of their comfort and space to keep domestic animals. Domestic husbandry,

whether it is poultry, rabbits or (less often) larger farm animals can provide an important source of food. For example, in **Study 1**, we showed that keeping backyard poultry positively influenced house sparrow abundance. Similarly, Šálek et al. (2015) demonstrated that the presence of house and tree sparrows was significantly affected by the frequency of poultry keeping. More recently, Kos et al. (2021) emphasized the importance of poultry, along with domestic and farm animals, for the occurrence of breeding birds. Furthermore, according to Havlíček et al. (2022) poultry provided a key food source, encouraging house sparrows to fly greater distances in search of it. However, it is worth noting that impact of domestic husbandry and livestock farming on bird populations has been relatively recently identified as under-investigated (Musitelli et al. 2016).

The availability of leftovers and discarded food might be another important food source influencing house sparrows abundance in urban areas. Even small food sources can attract large numbers of house sparrows, as seen in many cities worldwide. Cafés and restaurants with outdoor seating often draw flocks of sparrows feeding on leftovers (Fig. 1). Additionally, urban waste collection techniques play a significant role. For example, Bernat-Ponce et al. (2018) showed that house sparrows were most abundant in urban areas where rubbish bins were available as their foraging sites. As many countries transition from surface rubbish containers to underground ones, it's important to consider how this shift impacts sparrow populations. Recently, the same authors found that house sparrows were more abundant near surface bins compared to underground ones, likely due to higher food debris availability (Bernat-Ponce et al. 2022b).

In addition to the availability of anthropogenic food sources, green spaces play a crucial role in supporting house sparrow populations. Even a small amount of green space can have an impact on bird numbers in cities (Strohbach et al. 2013). In **Study 1,** we showed that greenery positively influenced house sparrow abundance. For most of the year, their diet is plant-based, but during the breeding season, invertebrates are necessary to feed their nestlings. Sufficiently vegetated space provides a source of invertebrates (Turrini & Knop 2015) and, moreover, woody plants (trees and shrubs) are important in providing shelter, especially for adult house sparrows during the breeding season (Vincent 2005). In addition, a lack of green spaces can increase predation risk and reduce small sparrow populations (Summers-Smith 2003).

Several studies cited **Study 1** in the context of the importance of vegetation cover (Strubbe et al. 2020, Mohring et al. 2021, Delahay et al. 2023). Mohring et al. (2021) found that house sparrow numbers were higher at sites with abundant green

spaces in opposition to census sites with no green spaces. In addition, in their recent review on the biodiversity in residential gardens, Delahay et al. (2023) stressed that even urban-adapted species such as house sparrows may be at risk from trends in residential development. They state that increasing housing density reduces the average individual garden plot size, and although the cumulative area of garden habitat may remain the same, connectivity could be impaired by the presence of more barriers to species dispersal. Furthermore, Bernat-Ponce et al. (2020) showed that the replacement of semi-natural cover with artificial substrates in urban parks causes a decline in house sparrows in towns. Indeed, it has been suggested earlier that tidy gardens with a high proportion of paved areas constitute less suitable habitats for foraging birds and may cause problems for adult house sparrows in the breeding season when insect-based food is required for nestlings (Shaw et al. 2008).

Fig. 1. House Sparrows feeding on leftovers in Riga (Latvia)

In conclusion, the survival and reproductive success of house sparrows in urban environments are closely linked to both anthropogenic food sources and the availability of green space, with a synergistic effect. While human activities may provide essential food resources, the presence of vegetated areas plays an equally crucial role as it promotes invertebrate availability and provides shelter, especially during the breeding season.

Role of vegetation structure (habitat heterogeneity) in bird diversity on restored sites

Study 2 was published a few years ago, in 2021, in the journal Landscape and Urban Planning and has already been cited 41 times according to Google Scholar and 23 times according to Web of Science (as of October 2024). Most studies cite this study to highlight the importance of habitat heterogeneity (vegetation structure) for a variety of species (Elliott et al. 2022; Ortí et al. 2022; Stukenholtz et al. 2022; Torresani et al. 2023; Torresani et al. 2024). Other studies simply used that paper to describe the possibilities of using lidar (Tamburlin et al. 2021; Khosrokhani et al. 2022; Štroner et al. 2023) or hyperspectral data (Anderle et al. 2023; Nguyen et al. 2023) for various purposes, including restoration assessment (Yuan et al. 2023).

Five years ago, Bakx et al. (2019) reviewed studies that adopted lidar for studying avian diversity. At that time, they found around fifty studies, and the numbers have been growing ever since, including also our **Study 2** as appreciated by one of the reviewers: "*The work presented is methodologically sound and provides a valid contribution to the ever-growing body of work using remotely sensed data to examine bird habitat and species diversity relationships.*" Indeed, habitat heterogeneity derived from lidar point clouds continues to be increasingly used in studies on bird diversity and distribution in various environments. I can name a few that have referred to our study. For example, Anderle et al. (2023) used lidar and multispectral data to assess the importance of habitat heterogeneity for birds in the agricultural landscapes of the central Alps. McNeil et al. (2023) concentrated on the Golden-winged Warbler, an early successional obligate, the populations of which have been declining for decades due to the loss of its nesting habitat – young forests. Suárez-Castro et al. (2022) studied the effects of landscape composition and configuration on diversity of urban birds. **Study 2** is, however, unique because it uses a specific environment of spoil heaps, as also highlighted by other reviewer: "*I have not seen a paper that would have addressed the restoration success of a site with lidar and field data together, which makes this paper just a tad more practical. I also enjoy the fact that you are referring to the evident increase in national lidar scanning campaigns: the data could and should be used in a more versatile way with ecology and environmental sciences. This paper provides one nice example.*"

The positive response to **Study 2**, particularly to its novel use of lidar and field data to evaluate restoration efforts, led us to conduct **Study 3** as a continuation of this research. In **Study 3**, we focused on aspects that were not included in **Study 2**, namely how different functional groups (i.e., guilds) respond to habitat

heterogeneity on reclaimed sites and surrounding areas. While **Study 2** provided valuable insights into species richness and habitat heterogeneity, **Study 3** shifted the focus to understanding how different bird guilds, based on their ecological roles, are affected by the complexity of vegetation and terrain on and in the proximity of restored sites.

The main novelty of **Studies 2 and 3** lies in demonstrating how remote sensing, particularly airborne lidar and hyperspectral data, can be effectively utilized to assess the status of restoration efforts, particularly in relation to habitat heterogeneity. However, very few studies cited our study in this regard (e.g. Yuan et al. 2023). In addition, both **Studies 2 and 3** underscored the importance of designing areas with diverse habitat heterogeneity and demonstrated how different restoration techniques contribute to it. In **Study 2,** we showed how habitat heterogeneity (more specifically vegetation characteristics) varied between areas restored using different restoration techniques, and several studies have cited **Study 2**, specifically emphasizing the importance of adopted restoration approaches and the associated complexity of vegetation structure (e.g., Korejs et al. 2024; Mukundi et al. 2024). For example, Elliott et al. (2022) highlighted the need for optimizing the understory and groundcover plantings to maximize the biodiversity outcomes of restoration as they support important ecological functions (such as nutrient cycling) and provide important animal habitats. Similarly, Lim et al. (2022) highlighted that selecting plant species can contribute to restoring spoil heaps into a multilayered forest and, in turn, increase biodiversity. I believe that **Study 3**, which concentrates on differences in habitat heterogeneity between restored areas and their unaffected surroundings, will be equally successful and useful for many studies that will come.

The analysis of vegetation structure and bird community evolution on spoil heaps over time is one area in which this research could be extended further. Partly, it is addressed by Korejs et al. (2024) who examined bird community development over 9 years (years 2012, 2019, 2020, and 2021) to analyze the response of the bird community to vegetation characteristics associated with different types of restoration management. In their study, however, the vegetation structure was derived from a field survey without using remote sensing methods. Since we have airborne laser scanning data available for 2012, 2017, and another scan planned for 2025, we could complement this study by examining the evolution of the bird community and vegetation structure more comprehensively. It is also important to note the discrepancy between the timing of species occurrence data acquisition and airborne laser scanning, the implications of which are discussed in detail in **Study 2**. Simply put, is more challenging to conduct the research when fieldwork

and scanning are not planned together. For research like this, they should be coordinated, rather than relying on the opportunistic use of data without prior planning, as was the case in our studies. The planned 2025 lidar scanning campaign gives us a great opportunity to address this issue.

Vegetation structure in urban environments

In the future, I would like to use lidar data for studies in urban environments. Although a considerable amount of data exists to describe urban vegetation, which could be useful for studies such as **Study 1**, those data have significant limitations. Data provided by municipal authorities often focus on widely recognized, formal categories of urban green spaces, such as parks, forests, and cemeteries. However, many other forms of urban greenery go unrecognized, either because they are located on private land or they are viewed as less important (Feltynowski 2023). Field surveys based on self-estimation are time-consuming (Ortí et al. 2022), and freely available remote sensing datasets are often limited in classification accuracy or spatial resolution (e.g. Venter et al. 2022).

Therefore, in **Study 1** we estimated vegetation cover (trees and shrubs) using orthophoto images. However, such an approach was only possible due to the relatively coarse resolution (i.e., 4 hectares) of our study plots, their relatively low number (125 plots), and the use of a simple metric describing overall greenery cover, thus not distinguishing between vegetation of different height, such as trees or shrubs. However, this does not allow the inclusion of a third dimension (height), which plays an important role for most, if not all, birds. Therefore, in **Studies 2 and 3**, we used the by far most accurate approach and derived vegetation cover on a spoil heap from lidar point clouds. This allowed us to distinguish different vertical layers of vegetation (e.g., understory and canopy cover).

Urban studies require high spatial resolution of mapping products as well as data on vegetation height and structure, such as those used in **Studies 2 and 3**. Unfortunately, the use of lidar in urban environments faces some limitations. In rural environments such as spoil heaps or forests (Fig. 2), the classification of lidar returns is relatively straightforward, as most come from the terrain and vegetation and terrain detection algorithms are relatively successful (Klápště et al. 2020). Still, buildings and, especially, high-voltage power lines (that can be misclassified as vegetation) can be problematic (Shi and Kissling 2023). In an urban environment, the situation is different as many objects can be misclassified in addition to the same objects as in rural environment, such as cars, objects on the roofs, or

streetlamps. This can make automatic detection of greenery difficult (Fig. 2; Huo et al. 2018) so a fully automated approach is currently impossible. However, if these difficulties are overcome by developing new, more accurate, algorithms, lidar data are an ideal source of vegetation structure in urban environments as well (e.g., Caynes et al. 2016; Sasaki et al. 2016; Choi et al. 2021).

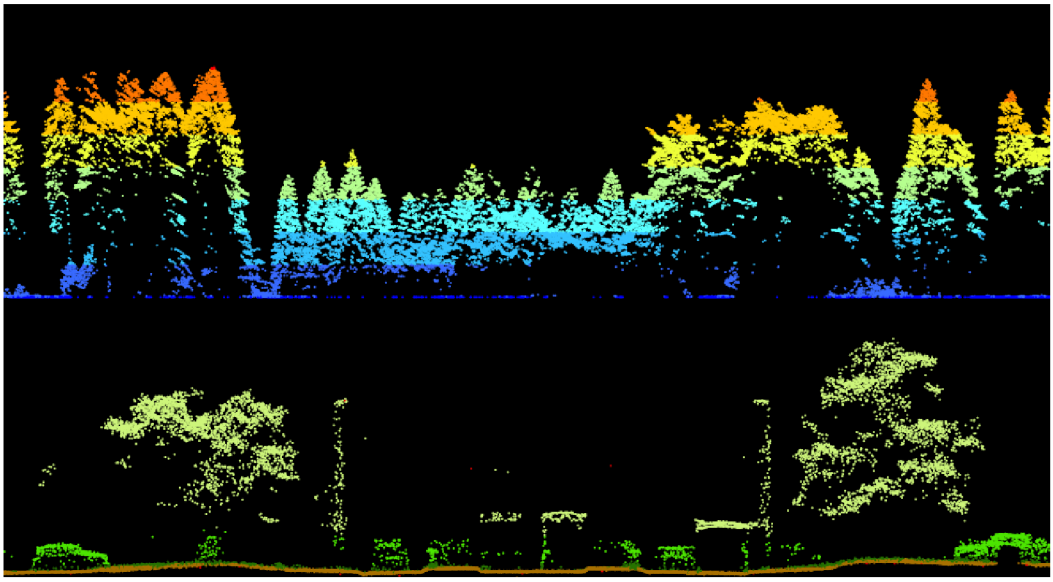

Fig. 2. Profiles acquired from lidar point clouds in forest (top) and city center (bottom) environments. Note the cars and streetlamps in the bottom image that might complicate the identification of vegetation returns.

Less time on environmental variables, more time for birds

We have spent a lot of time collecting and processing data; hence, I will allow myself a little reflection here, based on the experience of working on two different studies in terms of data collection and processing. Environmental variables affecting species diversity and distribution are commonly acquired during field surveys, ideally in the same period, which increases the demands on the observer. The field observations of environmental characteristics, besides being extremely time-consuming, might be subjective and, therefore, may be of only limited informative value. Moreover, such data are inevitably limited to relatively small areas and, thus, the inferred relationships between species and environment

cannot be used, for example, to predict species occurrence at other locations. Recently, McNeil et al. (2023) showed that models fitted with lidar-derived variables performed much better than those using only field-measured vegetation variables. Indeed, modern technologies such as remote sensing can save the time required for recording environmental characteristics in favor of collecting bird (species) data. Experienced ornithologists do not have to spend considerable time in the field collecting environmental characteristics but can devote their time to collecting bird data and exploring larger (or more) areas. Moreover, in urban areas where many sites are not publicly accessible, it may be difficult to correctly acknowledge many aspects of the environment (although birds can be acoustically identified with good accuracy). For example, the closed courtyards of blocks of buildings may hide parking lots, greenery, or community gardens that can have a significant impact on bird populations but can be recorded only from above, not from the street level.

Conclusions

Birds in human-altered environments have been gaining more attention in the last decades, not only from scientists but also from the general public. This thesis focused mainly on birds in an environment that has undergone a complete transformation due to human intervention, namely urban areas and spoil heaps. It contributes valuable insights into urban ecology and restoration practices, offering practical guidance for conservation planners and policymakers. By identifying key factors of habitat heterogeneity, this research can help optimize human-altered environments to support biodiversity. Moreover, the use of remote sensing technology provides a scalable tool for monitoring habitat quality, which could be integrated into large-scale restoration and conservation projects.

From the results of the thesis, the following conclusions can be drawn:

The number of house sparrows was significantly higher in the old built-up areas than in the newly built-up areas; this trend did not change even with the age of the newly built-up areas.

Sufficient green space (i.e. the tree and shrub cover) and backyard poultry are both important factors related to house sparrow abundance. Moreover, house sparrow abundance was higher where other granivorous species were present.

Sites left to spontaneous succession play an important role in creating restored ecosystems of high ecological value as they represent a unique combination of vegetation density and senescent vegetation that, in combination, promote high bird species rarity.

Creating a mosaic of habitats with heterogeneous vertical structures during restoration can be used to increase diversity or support preferred species or groups of species.

Canopy and understory nesters and foragers respond positively to vegetation structure, while ground nesters are particularly influenced by factors related to vegetation senescence and terrain characteristics.

Vertical variability of the vegetation in combination with the cover of senescent vegetation are potentially relevant metrics for monitoring habitat heterogeneity on restored sites using airborne remote sensing data.

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Curriculum Vitae & List Of Publications

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Education:

2010 – present **Czech University of Life Sciences Prague**, Faculty of Environmental Sciences, PhD programme: Applied and Landscape Ecology. *The effects of modern housing development on urban birds populations.*

2008 – 2010 **Czech University of Life Sciences Prague**, Faculty of Environmental Sciences, Master programme: Engineering Ecology (Applied Ecology). Diploma thesis theme: *Density of House Sparrow (Passer domesticus) population in different types of habitats: the impact of changes in the rural settlement and agriculture.*

2005 – 2008 **Czech University of Life Sciences Prague**, Faculty of Environmental Sciences, Bachelor programme: Applied Ecology.
Bachelor thesis theme: *Ecology and Protection of House Sparrow (Passer domesticus) in the Urban and Suburban Habitats.*

Work experience and training:

2017 – 2024	**Maternity leave.**
2015 – 2017	**Research assistant**: Department of GIS and Remote Sensing; Institute of Botany of the CAS, v. v. i.
2014 – 2015	**Research assistant**: Memorial University of Newfoundland, Canada
2014	**Coordinator**: The Spring Alive campaign, Czech Society for Ornithology
2012 – 2014	**Coordinator**: Assessment and reporting under Article 12 of the Birds Directive, Czech Society for Ornithology, cooperation with Nature Conservation Agency of the Czech Republic.
2012 – 2014	**Co-coordinator**: The "Hurá na vysokou" project, Czech University of Life Sciences Prague.
2010 – 2017	**Teacher, thesis supervisor and consultant**: Czech University of Life Sciences Prague.
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Publications:

Morelli, F., Brlík, V., Benedetti, Y., Bussière, R., **Moudrá, L.**, Reif, J., & Svitok, M. (2022). Detection rate of bird species and what it depends on: Tips for field surveys. *Frontiers in Ecology and Evolution*, *9*, 671492.

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