Czech University of Life Sciences Prague

Faculty of Environmental Sciences

Department of Ecology

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Farah Abou Zeid, M.Sc.

Exploring the effects of urbanization on bird species in European cities.

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Czech University of Life Sciences

Faculty of Environmental Sciences

Department of Ecology

Applied and Landscape Ecology Program

Community Ecology and Conservation Research Group

Ph.D. candidate: Farah Abou Zeid, M.Sc.

Advisor: Doc. Federico Morelli, Ph. D.

Consultant: Dr. Yanina Benedetti, Ph. D.

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Declaration

I confirm that this Ph.D. thesis is my original work, conducted under the supervision of doc. Federico Morelli, Ph.D., and Dr. Yanina Benedetti, Ph.D. Apart from contributions from co-authors in the enclosed papers and manuscripts, I have written this thesis independently. My involvement in the research and manuscripts is detailed in the authors' contributions and reflected in the authorship order of the published works. All relevant literature sources have been properly cited. This thesis, or any part of it, has not been submitted for any other academic degree or title.

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ABSTRACT

As urbanization expands, understanding its adverse effects on ecosystems, communities, and species becomes increasingly necessary. Birds are often the focus of urban ecology studies due to their ease of observation and role as effective bioindicators. Bird species vary in their responses to urbanization. While rare, specialist, and endemic species often suffer, a few widespread generalists thrive in urban areas, such as many corvid species. The replacement of native species with a few generalists leads to the biotic homogenization of urban avian communities. Understanding the factors that promote the presence of certain species and deter others becomes vital to urban conservation efforts.

In this compilation thesis, we examine various aspects of urban avian communities, including habitat selection and overlap, antipredator behavior, and the role of remote sensing techniques in monitoring avian diversity. The work was conducted during the breeding seasons in several European cities over multiple years. The scale of the studies ranged from single species in one city to entire urban bird communities across several European cities. Fieldwork consisted of different methods, from point counts to survey species presence and abundance to measuring Flight Initiation Distance (FID), the distance at which an individual initiates escape from a potential predator. We also used remote sensing indices like the Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) to assess the vegetation cover. The statistical methods employed various techniques and models.

We studied the urban habitat selection and overlap of corvids. We also investigated the impacts of urban noise pollution on the antipredator behavior of the Eurasian Magpie (*Pica pica*). Additionally, we examined the role of refuge availability, proximity, and type on the antipredator behavior of urban avian communities. Finally, we explored the capacity of specific remote-sensing vegetation indices to act as proxies for urban avian diversity beyond simple bird richness, potentially revealing homogenization.

Our findings showed a high overlap in the habitats of all corvid species despite some specific preferences. The corvids with similar habitat preferences often co-occurred, indicating low competition. Urban noise did not significantly affect the Magpies' ability to detect danger, but it did slow their reaction and escape. We found that urban birds preferred to seek refuge in trees after disturbance and felt more secure when near potential refuges, delaying their flight after disturbances. Finally, the NDVI mean proved to be a good proxy for multifaceted avian diversity monitoring and could help identify potential homogenization.

This thesis contributes to the growing field of urban ornithology, providing insights to guide conservation efforts. In Europe, urban ornithology can inform strategies to reduce avian loss and provide valuable knowledge for urban planning in newly developing cities worldwide to preserve biodiversity.

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CHAPTER 1.   INTRODUCTION

1.1- The role of birds in ecological studies

Across cultures and throughout history, birds have consistently assumed the role of literary messengers, symbolizing various emotions due to their captivating beauty and ability to soar free in the skies (Cocker, 2014; D'couto, 2016; Serjeantson, 2009; Tidemann & Gosler, 2012). Beyond their symbolic significance in literature, birds are a key component of scientific inquiry, enabling people to answer some of the most complex questions about the world. Bird study, also known as ornithology, is one of the earliest established scientific fields, making birds some of the most researched organisms (Birkhead et al., 2014; Del Hoyo et al., 1992; Tietze, 2018). Many factors allowed birds to feature frequently in scientific research. First, their ease of study has attracted ecologists due to their high detectability, abundance, spread, and established phylogenies (Jetz et al., 2012; Prum et al., 2015). For several reasons, birds can also be used as model organisms for other species. First, they are model organisms for population studies due to the high diversity of their social systems (Konishi et al., 1989). Moreover, they use similar senses to humans, making them ideal subjects for neurological studies (Konishi et al., 1989). Birds are likewise often considered reliable bioindicators for other taxa, ecosystems, and habitat quality (Benmazouz et al., 2021; Goodness et al., 2016; Morelli, Reif, et al., 2021). Avians also play significant and diverse roles in ecosystems due to their valuable functions (Gaston, 2022). Thus, they directly or indirectly benefit humanity through the various ecosystem services they support, namely regulating, provisioning, supporting, and cultural services (Lees et al., 2022). Many bird species act as pollinators, seed dispersers, scavengers, and ecosystem engineers (Goodness et al., 2016; Heyman et al., 2017). Through migration, birds preserve ecological connections, linking ecosystem processes between distant areas (Graham et al., 2018). Therefore, bird studies help unfold the diverse functions of birds, contribute to the knowledge of different fields like behavior, evolution, and biology, and monitor ecosystem function and quality across time (Tietze, 2018). Though the field is reasonably established and bird species are relatively well understood, anthropogenic impacts, through land use alterations and climate change, pose new challenges to bird species, forcing them to adapt or suffer (Tietze, 2018).

1.2- Ornithology in urban environments

Urbanization is defined as anthropogenically caused landscape alterations resulting from the development of human settlements (i.e., cities) and is one of the most severe causes of human-related impacts on ecosystems (Foley et al., 2005). Around 55% of the global population currently resides in urban areas, and this number is projected to increase to 68% by 2050 (UN DESA, 2019). Specifically, in Europe, 75% of the people live in urban areas, which is expected to reach 84% by 2050 (UN DESA, 2019). Likewise, urban areas are predicted to continue to grow rapidly and are, thus, one of the fastest-expanding land-use types (McDonald, 2008). Even though urban areas occupy only 3% of the global land cover (Z. Liu et al., 2014), the adverse impacts of urbanization can affect areas many times their size (McGranahan & Satterthwaite, 2003) by depleting their natural resources, for example (Czech et al., 2000). Furthermore, urban land is shown to grow faster than the population and is expected to double in size within 19 years (Angel et al., 2011).

Ornithology has emerged as a prominent discipline in urban studies driven by the rapid expansion of urban areas and the imperative to understand their profound impacts on ecosystems, communities, and species (Collins et al., 2021). A deeper understanding of the adverse effects of urbanization would contribute to informing more sustainable urban planning strategies (Lepczyk & Warren, 2012; McCloy et al., 2024). Birds have become central to urban ecological studies due to their abundance in cities and ease of observation across various spatial scales (Mekonen, 2017). Furthermore, bird communities exhibit dynamic responses to urbanization, offering valuable insights into its broader environmental impacts (Lepczyk & Warren, 2012). Avian communities also serve as bioindicators of urban ecosystems' health, guiding efforts to mitigate and reduce the adverse effects of urbanization on ecosystem functioning (McCloy et al., 2024; Mekonen, 2017; Morelli, Reif, et al., 2021).

Preserving urban biodiversity (a major facet of urban green infrastructure) is necessary to ameliorate the well-being of human urban populations (Elmqvist et al., 2013; European Commission, 2011; Hedin et al., 2022). Not only is biodiversity critical for biomedical research and drug development (Chivian & Bernstein, 2004), but it also provides health benefits for people on a local scale (Hedin et al., 2022; Taylor & Hochuli, 2015). For example, urban green spaces with complex and diverse species provide people with various psychological benefits (Fuller et al., 2007). Bird watching is one of the many cultural services birds offer to people due to their aesthetic and symbolic values. Increased bird diversity, bird-watching activities,

and listening to bird songs improved positive affect and vitality and diminished anxiety levels and mood disorder hospitalization in the population (Buxton et al., 2023; Cox et al., 2017; Cox & Gaston, 2016; Ratcliffe et al., 2013; Wolf et al., 2017). Enhancing the well-being of the urban population becomes necessary as the urban populations continue to grow.

For all these reasons, the field of urban ornithology has been flourishing, specifically in Europe, the United States of America (hereafter "USA"), and Canada (Collins et al., 2021; Marzluff, 2017).

Europe's long urban history presents a unique opportunity for avian ecological studies aiming to understand the complex relationships between wildlife and urbanization (Jokimäki et al., 2016). Such studies can reveal the various adverse species-specific effects of urbanization and the effects on the overall community structure. Urban ecological studies in Europe can offer valuable knowledge and instruct urban planning initiatives toward more sustainable cities. Such information would greatly benefit newer, currently developing, and expanding cities worldwide, guiding the development of biodiverse and wildlife-friendly cities (Jokimäki et al., 2016). Understanding the adverse effects of urbanization on birds in Europe can help mitigate these impacts and reduce avian loss. The abundance of native European birds has declined between 17% and 19% since the 1980s (Burns et al., 2021). This heavy loss is mainly attributed to anthropogenic land-use changes, including urbanization and agricultural intensification (Burns et al., 2021; Fusco et al., 2021).

1.3- The impacts of urbanization on birds

Urban growth heavily alters the landscapes (Güneralp et al., 2020), destroying, fragmenting, or modifying species' natural habitats (Aronson et al., 2014; Fernandez-Juricic & Jokimäki, 2001). Not only does urbanization alter the landscape with impervious structures (i.e., roads and buildings), but even remaining green areas in cities tend to differ from the original natural habitats of species since people plant non-native species, remove midstory canopy, and manage lawns (Aronson et al., 2014; Luck & Smallbone, 2010). Habitat destruction and fragmentation are likely the primary risk factors urbanization poses on bird species, forcing them to either look for more suitable habitats or adapt to the new conditions (Isaksson, 2018; Marzluff & Ewing, 2008; Mckinney, 2002).

Besides changing the landscapes, urbanization also introduces additional risk factors for species. For one, urban areas are associated with higher levels of air pollution from various

sources, such as vehicular fuel combustion, power and heat generation, and municipal waste (Coelho et al., 2022). Air pollution has been shown to adversely affect the fitness of birds either directly or indirectly. Birds' respiratory systems are susceptible to air quality due to their efficiency in allowing the uptake of aerially suspended compounds (Brown et al., 1997). The impacts of inhaling air pollution include increased oxidative stress, susceptibility to illness, reduced thyroid function in birds, behavioral changes, and reduced reproductive success (Sanderfoot & Holloway, 2017).

Urban areas are also associated with increased ambient noise levels, attributed primarily to traffic characterized by low-frequency sounds (Warren et al., 2006; Zollinger et al., 2017). Many species use sounds for communication and survival; therefore, they are not inherently harmful (Sordello et al., 2020; Sun & Narins, 2005). Elevated sounds may escalate to "noise pollution" when they disrupt wildlife, although different species may have varying tolerance levels (Sun and Narins, 2005; Sordello et al., 2020). Birds are a prime example of fauna negatively impacted by noise pollution. Avians depend on acoustic communication and signals to navigate their environment (Francis et al., 2009; Hu & Cardoso, 2009; Petrelli et al., 2017). They use their songs to communicate with brood and conspecifics, attract partners, and assert dominance (Catchpole & Slater, 2003; Slabbekoorn & Ripmeester, 2008). Birds rely on acoustic cues to detect approaching predators and send and receive signals from or to conspecifics about such potential predatory threats (Hollén & Radford, 2009). Therefore, missing calls from conspecifics can inflict fitness costs on the birds, such as missing mating calls from an optimal mate or missing alarm calls about an approaching predator (Brumm & Zollinger, 2013). Despite the adverse impacts of sound masking on bird communication, many bird species could adapt to the novel soundscapes within urban areas in various ways. For instance, some birds were found to modify the timing of their songs, starting at earlier times during the day to avoid the rush hour (Dorado-Correa et al., 2016). Some urban birds were demonstrated to sing at higher frequencies to minimize masking by low-frequency traffic noise (Bermúdez-Cuamatzin et al., 2011). The reflexive increase in song amplitudes to maintain the signal-to-noise ratio, known as the Lombard effect (first identified in humans and later observed in other animals), is another way urban birds react to increased noise (Brumm, 2004; Lombard, 1911). Finally, some urban bird species were observed to sing longer songs in urban areas (Ríos-Chelén et al., 2013). Such modifications may result from phenotypic plasticity or natural selection (Ríos-Chelén et al., 2012; Warren et al., 2006).

However, besides masking sound cues, noise exposure entails direct physiological impacts by disrupting sleeping patterns and elevating stress levels (Grunst et al., 2021). Elevated stress from chronic exposure has been shown to weaken the immune system, increasing the individual's vulnerability to illness and diseases (Berkhout et al., 2023). Such diverse effects of noise pollution can result in detrimental outcomes from individual fitness to population dynamics and community structure (Francis & Barber, 2013).

Another form of widespread pollution in urban regions is light pollution, namely the increased Artificial Light at Night (hereafter "ALAN"). Light pollution is defined as the adverse impacts of the extreme and disproportionate use of light (Ryer, 1997). Animals are accustomed to the regular patterns of light and darkness, giving the light a primary role in regulating daily and seasonal behavioral and physiological cycles (Dominoni et al., 2013; Gwinner & Brandstätter, 2001). ALAN exposure may, therefore, disrupt organisms' circadian clock, leading to cascading effects, from disturbed hormone production to disrupted sleep, immunosuppression, stress, and more (Dickmeis, 2009; Figueiro & Rea, 2010; Grunst et al., 2020; Navara & Nelson, 2007; Raap et al., 2016). Birds exposed to light pollution were shown to extend their activity timing, starting to sing earlier in the morning and ending later at night (Da Silva et al., 2015; Da Silva & Kempenaers, 2017). They also spend more time foraging and increase their activity at night (Russ et al., 2015). These changes are energetically costly and negatively impact the birds' fitness (Da Silva et al., 2015; Raap et al., 2016). ALAN was shown to advance avian reproduction behavior, leading to a mismatch between optimal resource availability and clutch nutritional needs (Dominoni et al., 2013; Kempenaers et al., 2010). Thus, urban light pollution's impact on species may vary depending on their dietary needs, where omnivores and insectivores are adversely affected but not granivores (Morelli et al., 2023). Birds are naturally attracted to light, leading to millions of deaths yearly due to collision with artificial light structures (Gauthreaux Jr et al., 2006; Longcore et al., 2008). Light pollution also interferes with birds' migration, causing them to become disoriented (Horton et al., 2019). However, light pollution may have a few benefits, as some birds exploit artificial light structures to prey on insects that may be trapped there (Robertson et al., 2010).

Urban birds are subjected to increased predation by human companion animals, mainly domestic cats (*Felis silvestris catus*, hereafter "cats") and dogs (*Canis lupus familiaris*) (Rebolo-Ifrán et al., 2021). Additionally, collision with human-made structures, such as windows, increases birds' vulnerability to predation by cats and dogs (Rebolo-Ifrán et al., 2021). Besides directly killing the birds through predation (Beckerman et al., 2007; Greenwell

et al., 2019), these mesopredators inflict fear-related sublethal effects on avian species' adversely impacting their behavior, habitat selection, feeding, and fertility (Dauphiné & Cooper, 2009; Greenwell et al., 2019; Pavisse et al., 2019). Birds have decreased densities, even within their ideal niches, in the presence of cats or their cues (i.e., feces, urine, or fur; Apfelbach et al., 2015; Kosicki, 2021). Furthermore, cats are vectors for various diseases that threaten wildlife and people alike (Dauphiné & Cooper, 2009; Greenwell et al., 2019). According to the International Union for Conservation of Nature (IUCN), cats have caused or facilitated the extinction of sixty-three species of birds, mammals, and reptiles (Nogales et al., 2013). In the USA alone, estimates show that cats kill between 1.3 and 1.4 birds annually (Loss et al., 2013). Consequently, cats are the main direct human-related factor behind avian mortality (Loss et al., 2013). Specifically, fledglings are often at increased risk of cat predation, reducing urban birds' breeding success (Heyman et al., 2017). Cavity-nesting and ground-foraging species are often the preferred targets for these predators (Bonney et al., 2009). As for dogs, they pose threats to more than 78 bird species worldwide (Doherty et al., 2017).

The long list of challenges birds face in urban environments also includes mortality risks due to collision with buildings, windows, and vehicles and increased risks of illness, among others (Hager et al., 2017; Kent et al., 2021; Santiago-Alarcon & Delgado, 2017; Van Doren et al., 2021).

On the other hand, urban areas present advantages for certain bird species. These areas offer abundant anthropogenic food resources and artificial nesting sites (Gil & Brumm, 2013; Mainwaring, 2015; Marzluff, 2001). For instance, buildings serve as safer nesting sites for some bird species, where they often experience higher reproductive success than nesting outdoors (Møller, 2010). In addition, many species seek urban areas for warmer temperatures, resulting from the Urban Heat Island (hereafter "UHI") effect (Isaksson, 2018). The UHI effect is caused by the increased temperature in urban areas compared to non-urban ones due to the heat-retaining qualities of the impervious surfaces and buildings, the heat-trapping impact of air pollution, and reduced green cover (Oke, 1982). Due to the UHI effect, cities attract early-arriving migratory birds (Tryjanowski et al., 2013).

By altering the physical, biotic, and abiotic environment and introducing new challenges, urban areas modify the species' community compositions as well (Aronson et al., 2014; Fernandez-Juricic & Jokimäki, 2001; Morelli et al., 2016). Many species fail to withstand the novel conditions and disappear in urban environments (Marzluff, 2001). Particularly, specialists (species that can only prevail within a narrow set of environmental factors; Hutchinson, 1957;

Whittaker et al., 1973), native, and endemic species are the most severely affected. On the other hand, many generalists (species that can tolerate a wide range of conditions; Hutchinson, 1957; Whittaker et al., 1973) can exploit the new conditions and unoccupied niches. Ultimately, the replacement of native, endemic, and rare species with a few widespread generalists leads to the biotic homogenization of urban communities (McKinney, 2006; McKinney & Lockwood, 1999). Biotic homogenization is when city avian communities become more similar to each other than to those of nearby regional ecosystems (i.e., in Europe; Ferenc et al., 2014). Many studies demonstrate that bird species richness declines with increased urbanization while abundance increases (Chace & Walsh, 2006; Kontsiotis et al., 2019; Marzluff, 2001). However, some studies show that avian richness peaks at intermediate levels of urbanization (Blair, 1996). Still, even with increased richness, these urban communities are made of redundant species present in cities worldwide (Kontsiotis et al., 2019). These are mainly cosmopolitan species and include Feral Pigeons (*Columba livia*), House Sparrows (*Passer domesticus*), and others (Aronson et al., 2014). Even when the urban species communities differ, they are overrepresented by the same few families (i.e., pigeons and corvids; Sol et al., 2017). Therefore, urbanization leads to declining global biodiversity (Aronson et al., 2014). Urbanization-caused biotic homogenization can be observed at different levels. It was shown to cause taxonomic, functional, and phylogenetic homogenization of avian communities (Devictor et al., 2007; Godet et al., 2015; Ibáñez-Álamo et al., 2017; Morelli et al., 2016; Reif et al., 2013). Finally, a recent large-scale European study found that increased urbanization levels were associated with a decrease in the evolutionary distinctiveness of the bird species (Morelli et al., 2024).

1.4- Different ways avian species respond to urbanization

Due to species-level responses to urbanization, as an area becomes increasingly urbanized, the species composition will likewise be modified, with some species disappearing and others thriving (Isaksson, 2018). Therefore, birds can be classified into three groups based on their response to urbanization: urban exploiters, adapters, and avoiders (Blair, 1996).

Urban exploiters thrive in urban areas and take advantage of anthropogenic and artificial resources, such as plentiful food options and novel artificial nesting sites, like nest boxes and building holes (Blair, 1996; Kark et al., 2007; Liordos et al., 2021; Mckinney, 2002; McKinney, 2006). Urban exploiters, many of whom are invasive species, have utilized human resources to the point of now depending on them for survival (Isaksson, 2018). They prefer high grey cover

and human disturbance, usually located within city centers (Liordos et al., 2021). Urban exploiters do not rely on green cover and may be negatively linked to it (Mckinney, 2002). Alternatively, urban adapters are species that do not entirely rely on human resources but can still take advantage of them. Those species usually avoid city centers and reside within areas with green cover (Liordos et al., 2021). They seek regions resembling their natural habitats in urban areas, "adapting" to urbanization while still resorting to natural resources (McKinney, 2006). These species can out-compete urban exploiters in case of a decrease in anthropogenic resources, and the opposite is true (Isaksson, 2018). Finally, urban avoiders are the most sensitive species to environmental modifications and only thrive in their pristine natural habitats (Blair, 1996). They are the most easily identifiable as they disappear quickly once environments become urbanized (Isaksson, 2018). However, it is hard to classify some species for which urban areas may act as ecological traps (Lepczyk et al., 2017). Those species would be lured to urban regions due to the abundant food sources, artificial sites, and milder weather and would be tricked into viewing urban sites as high-quality environments (Lepczyk et al., 2017). Then, these birds would suffer from the many risk factors of urbanization that were previously elaborated (Donovan & Thompson, 2001). Urban areas jeopardize the survival of these birds and reduce their fitness, causing their populations to decline slowly over time (Donovan & Thompson, 2001). Thus, long-term population studies are necessary to identify these species at risk (Isaksson, 2018).

Understanding the factors and characteristics that allow certain species to thrive and adapt to urban areas while others suffer adverse consequences can be key to identifying vulnerable species and mitigation measures. While our understanding of the traits that make urban-tolerant birds is still limited, several factors have been shown to influence their ability to thrive in urban environments (Sayol et al., 2020). In general, urban tolerance is positively linked to dietary and habitat niche size (Callaghan et al., 2019; Ducatez et al., 2018; Lizée et al., 2011; Sayol et al., 2020), making generalists less vulnerable to anthropogenic alterations (Callaghan et al., 2023). Birds that nest high up in a tree are much more successful in urban regions than ground nesters (Conole & Kirkpatrick, 2011; Dale et al., 2015). Gregarious birds have also performed better in urban circumstances (Croci et al., 2008; Kark et al., 2007; Sol et al., 2014). Other characteristics that have been associated with urban birds such as dispersal ability (Møller, 2009; Neate-Clegg et al., 2023), larger clutch size (Lizée et al., 2011; Neate-Clegg et al., 2023), and longer life spans (Croci et al., 2008; Neate-Clegg et al., 2023). However, the importance

of many traits for urban tolerance determination may vary according to the region (Neate-Clegg et al., 2023).

Some behavioral characteristics such as boldness, innovation, and adaptability define urban birds (Patankar et al., 2021). Studies worldwide have revealed the role of phenotypic plasticity in the swift behavioral adaptations of avian species to urbanization (Marzluff, 2017). Urban areas provide ample food resources at the cost of increased human, cat, and dog presence. Therefore, only bolder individuals are expected to explore these resources. Indeed, studies have shown that urban birds are bolder than their rural conspecifics (Sol et al., 2011; Tryjanowski et al., 2016).

1.5- Behavioral adaptations through Flight Initiation Distance

One way to measure birds' risk-taking, behavioral adaptations, and flexibility in urban areas is through the Flight Initiation Distance (hereafter "FID"; Møller, 2021). More specifically, FID is used to study the antipredator behavior of species under various conditions. FID is the distance that separates the prey from a potential approaching predator (in ecological studies, usually a researcher that approaches under standard conditions) when the prey initiates escape (Blumstein, 2006). Alert Distance (hereafter "AD") is the distance before FID when the prey first notices the predator (Fernández-Juricic et al., 2002). After detecting an advancing predator, the prey must evaluate the danger level and choose a potential proper distance to flee (W. E. Cooper et al., 2015).

The optimal escape distance is difficult to determine for prey. Early escape would come at the cost of the loss of foraging opportunities or other tasks at hand. On the other hand, late escape would increase the predation risk and may put the individual's life in jeopardy. Therefore, the FID is a compromise between the risks of staying put and resuming the current activity and escaping and losing energy and opportunities (Møller, 2008). Thus, FID is expected to be the distance when it becomes more costly to stay than escape (Ydenberg & Dill, 1986). FID studies can, therefore, help determine the factors that impact the decision-making regarding when to flee that may push the tradeoff in either direction. Several factors have been shown to influence this decision and alter FID in birds and other species. First, the Starting Distance (hereafter "SD" or the distance separating the two individuals at the beginning of the approach) and the AD are positively linked to FID (Chen et al., 2020). Therefore, the SD must be controlled during the FID collection or accounted for during the data analyses.

Some functional traits seem to impact interspecific and individual FID variations. For one, body size has consistently been shown to reduce FID (Gnanapragasam et al., 2021; Morelli et al., 2019). Larger birds require more time to initiate flight due to their size than smaller individuals, which may prompt them to initiate escape earlier (Fernández-Juricic et al., 2006). Larger birds are more easily detectable and make a larger, more tempting meal to predators, increasing their risk of predation (Fernández-Juricic et al., 2002; Holmes et al., 1993). Human hunters have targeted larger birds more than smaller species, which may have increased their fear of people and, as a result, their FIDs (Gnanapragasam et al., 2021). Flock size has also been shown to affect FID either positively or negatively (Shuai et al., 2024). The impact may be affected or diminished by other confounding variables, such as body size and climate (Shuai et al., 2024). Environmental factors seem to influence FID as well. For example, birds may delay escaping the higher perched they are (Chen et al., 2020), when food abundance is low (Møller et al., 2015), and when temperature and precipitation are high (Díaz et al., 2021). Urban birds have consistently been shown to have shorter FIDs than rural ones (Møller et al., 2015; Morelli et al., 2019; Sol et al., 2018). Urban individuals have shorter FIDs than rural conspecifics of the same species (Carrete et al., 2016; Vincze et al., 2019). Due to human prevalence, birds are expected to exhibit reduced fear in urban environments, allowing them to prioritize activities such as foraging and reproduction over energetically costly constant fleeing (W. E. Cooper & Frederick, 2007; Tryjanowski et al., 2016). The difference between urban and rural FID may reveal the behavioral plasticity of urban individuals, enabling them to habituate to human presence and reduce their fear over time (Vincze et al., 2019). Alternatively, the local adaptation theory proposes that urban areas select for more courageous organisms (Møller, 2008). Finally, bolder rural individuals may have higher chances of successfully colonizing urban areas, as explained in the differential colonization theory (Carrete & Tella, 2011).

1.6- Corvids, successful urban dwellers

Many corvid species are some of the most successful urban exploiters, profiting significantly from anthropogenically modified habitats (Garcia-Porta et al., 2022; Matsyura et al., 2016; Preininger et al., 2019; Wang et al., 2008). Their intelligence allowed them to habituate to human presence and exploit the abundant resources associated with them (Seed et al., 2009; Sol et al., 2005). Studying corvids in urban areas can help identify traits that enable certain birds to adapt to these novel habitats while others do not. Moreover, corvids are a nuisance for

both people and ecosystems (i.e., they are noisy nest predators; Benmazouz et al., 2021; Madden et al., 2015; Marzluff & Neatherlin, 2006). However, some species may provide valuable ecosystem services in urban areas, such as seed dispersal, serving as biosensors for diseases, and reducing animal remains through scavenging (Benmazouz et al., 2021; Julian et al., 2002; Pesendorfer et al., 2016; Schwartz et al., 2018).

1.7- Monitoring avian diversity in urban environments

Knowledge of the spatial patterns of species distribution can provide valuable insights for developing sustainable land management practices and crafting more efficient conservation plans (Seto et al., 2004). Traditional field surveys can offer crucial information about the community composition, species distribution, and abundance, but they are costly, challenging, and time-consuming (Seto et al., 2004). Remote sensing tools using satellite images offer accessible ways to monitor variables correlating with biodiversity, such as by locating different land cover variables (Roughgarden et al., 1991; Turner et al., 2001). Such tools allowed the development of vegetation indices, such as the Normalized Difference Vegetation Index (hereafter "NDVI") and Enhanced Vegetation Index (hereafter "EVI"). NDVI is calculated using the near-infrared (that is reflected strongly by green vegetation) and red light (that is absorbed by the vegetation) spectral reflectance from the land surface (Huete et al., 1999). NDVI is an index between -1 and 1 that indicates vegetation presence and density (Pettorelli, 2013). EVI is calculated similarly but incorporates blue bands for atmospheric and background correction (H. Q. Liu & Huete, 1995). Both indices are used extensively to map vegetation, proving to be great proxies of its spatiotemporal distribution (Pettorelli et al., 2005) and primary productivity (Box et al., 1989). Higher NDVI and EVI values suggest healthier and denser vegetation (Matsushita et al., 2007). EVI and NDVI can effectively indicate avian diversity since primary productivity affects species diversity and distribution (Wright, 1983). These vegetation indices proved to predict avian species richness within and outside urban areas (Bae et al., 2018; Bino et al., 2008; Callaghan et al., 2020; W. J. Cooper et al., 2020; Hobi et al., 2017; Leveau, 2019). However, since species richness may increase despite biotic homogenization, their capacity to predict avian community composition remains unknown.

1.8- The value of urban ornithological studies

Due to the fast urban expansion, it is necessary to understand the various impacts of urbanization on species and communities to mitigate them (Díaz et al., 2022; Miller & Hobbs,

2002). Avian ecologists should, therefore, guide urban planners and policymakers to make informed urban growth decisions to preserve biodiversity (Marzluff, 2001). Furthermore, urban areas allow the study of various aspects of evolution, adaptation, and plasticity in species in real-time (Alberti, 2015; Isaksson, 2018) as they enable studying the impacts of rapid environmental changes on biodiversity (Alberti, 2015; Morelli, Benedetti, et al., 2021). Urbanization is also an example of the various anthropogenic pressures species have to endure, and therefore, urban ecology provides a means to study the impacts of these pressures on communities (Marzluff, 2017). This thesis aims to improve the understanding of urban bird communities and contribute to the field of urban ornithology. The objectives are better described in the next chapter.

CHAPTER 2.   AIMS AND OBJECTIVES

This thesis aims to improve the understanding of urban bird communities and contribute to the field of urban ornithology. The specific aims can be summarized as follows:

1- To investigate the habitat and behavioral adaptations of select urban-dwelling bird species

2- To understand some of the impacts of urbanization on the antipredator behavior of birds

3- To assess the capacity of some tools of remote sensing in monitoring large-scale urban avian diversity

In more detail, the objectives of each article are:

2.1- Research I (Annex I):

"Spatial overlap and habitat selection of corvid species in European cities"

This study aimed to characterize the habitat selection and the degree of spatial overlap among five corvid species inhabiting different European cities. Specifically, to assess:

2.1.1- The presence and distribution of each corvid species in 16 European cities:

This objective helps identify the most successful corvid species in European cities. Such information may highlight traits and behaviors of species that facilitate their proliferation in urban environments. Additionally, identifying the most and least successful corvid species coupled with other studies and the literature would determine whether there is a need to control or promote their presence in urban areas depending on their impacts (Marzluff & Neatherlin, 2006).

2.1.2- The level of spatial overlap among the five corvid species

This aim seeks to assess the extent of spatial overlap among the five corvid species within European cities. By analyzing their spatial distribution patterns, this research aims to determine whether the corvid species pairs' co-occurrence is coincidental, more likely than expected by chance, or less likely. Understanding the degree of spatial overlap provides insights into habitat resource partitioning, resource sharing, and competitive interactions among corvid species.

2.1.3- The level of overlap of their habitat selection

Here, we seek to comprehend the extent of habitat niche overlap among corvid species in European cities. Understanding niche overlap among sympatric species reveals their interspecific relationships, competition, and resource partitioning (Matsubara, 2003). While studies on niche overlap are quite common for specialist species, they remain rare for generalists, particularly in disturbed environments like urban areas (Matsubara, 2003). Finally, this investigation seeks to determine whether habitat preferences influence spatial associations. The influence may lead to positive (showing co-occurrence driven by similarity in habitats) or negative (suggesting avoidance due to high competition) spatial associations.

2.1.4- The urban features selected by each species

This objective will help identify specific urban features selected by each corvid species in European cities to highlight potential adaptations to novel environmental features the species may have undergone to thrive in urban regions. Alternatively, it may show similarities to their natural habitat preferences. Understanding urban habitat selection by corvids contributes to evolutionary studies and provides insights into urban ecosystem dynamics (Benmazouz et al., 2021; Marzluff & Neatherlin, 2006). It would also help shape urban planning efforts to control certain populations and promote higher urban diversity.

2.2- Research II (Annex II):

"Urban noise slows down the antipredator reaction of Eurasian Magpies"

In this research, we intended to explore the effect of noise pollution on Magpies' antipredator behavior in Prague during the breeding season. The specific objectives were to investigate:

2.2.1- The variation of AD and FID/AD of Magpies across a gradient of urban noise

Here, we wish to uncover the potential effects of urban noise pollution on Magpies' antipredator behavior. Urban noise may impact the antipredator behavior in two opposing ways. Urban noise can reduce the animal's vigilance by distracting it or masking the sounds of an approaching predator (Barber et al., 2010; Chan, David Stahlman, et al., 2010; Zhou et al., 2019). Alternatively, it may cause the animal to heighten its vigilance either to compensate for the reduced hearing capacities or because it fears the noise in itself (Evans et al., 2018; Kern & Radford, 2016; Meillère et al., 2015; Shannon et al., 2016). Such effects may be revealed in

the AD (reflecting threat detection) and a corrected FID (FID/AD, which demonstrates the speed of the response after threat detection).

2.2.2- *The consistency of the impact of noise on threat detection and speed of the escape response.*

We hypothesized that the two opposing ways noise may impact the antipredator behavior may not be exclusive and can thus manifest differently in two measures of fear. First, distraction may be observed in a reduced alert behavior, hence a smaller AD. However, the Magpies may increase their speed of response to the threat to compensate for their suppressed attention, which can be reflected in an increased FID/AD.

2.3- Research III (Annex III):

"Flight initiation distance and refuge in urban birds"

This study aimed to compare the escape distances (measured as FID) of birds concerning the:

2.3.1- *Distance to the closest potential refuge*

This aim investigates how the distance of birds to their nearest potential refuge affects their FID. We seek to determine whether proximity to the refuge provides birds with increased (or perceived) security, potentially reducing their FID since closer refuge needs less time to reach and, thus, less time to be captured.

2.3.2- *Distance fled to the refuge*

Here, we examine the association between FID and the Distance Fled (hereafter, "DF") to the actual refuge. This aim can determine whether fearfulness is a consistent personality trait for individuals that is displayed similarly across measures of fearfulness (W. E. Cooper & Frederick, 2007; W. E. Cooper & Wilson, 2007).

2.3.3- *Refuge type and availability in urban areas*

This aim focuses on how different types of refuges (i.e., trees, bushes, and artificial structures) impact the FID of birds. The goal is to determine if birds prefer certain types of refuge that may provide them with a sense of increased security (Lima, 1993).

2.4- Research IV (Annex IV):

"EVI and NDVI as proxies for multifaceted avian diversity in urban areas"

In this article, our objectives were to investigate the capacity of EVI and NDVI as proxies for different facets of avian diversity (i.e., measures of taxonomic, functional, and phylogenetic diversity, urban tolerance, and avian specialization) and determine the better surrogate in each case in 15 European cities:

Exploring the ability of these two vegetation indices to predict various bird diversity metrics may uncover cost-effective and efficient tools for large-scale urban diversity monitoring. It may also determine which index better represents specific aspects of biodiversity and highlights the significance of urban vegetation for avian diversity.

CHAPTER 3.   LIST OF PUBLISHED WORK

This thesis's core consists of peer-reviewed articles published in indexed scientific journals with Impact Factor (J_{imp}). The complete articles are provided in the Annex section:

Annex I. Spatial overlap and habitat selection of corvid species in European cities.

Annex II. Urban noise slows down the antipredator reaction of Eurasian Magpies.

Annex III. Flight initiation distance and refuge in urban birds.

Annex IV. EVI and NDVI as proxies for multifaceted avian diversity in urban areas.

The next Chapter, "Discussion," provides a commentary on these articles.

CHAPTER 4. DISCUSSION

My thesis comprises four articles published in indexed scientific journals. I am the first author of two articles and co-author of the remaining two. My first authored publications focus on corvids, a group of birds, many of which thrive in urban environments. In the first paper (see Annex I: Research I), we investigate the urban distribution, habitat selection, and habitat overlap of corvids in sixteen European cities during the 2018 breeding season. The data for this paper was obtained from a large project funded by the Czech Science Foundation GAČR (project number 18-16738S).

The second paper (see Annex II: Research II) moves to the behavioral ecology of urban corvids. Using the AD and FID, we investigate the impacts of urban ambient noise pollution on the antipredator behavior of Eurasian Magpies (*Pica pica*, hereafter "Magpie") in Prague in the 2022 breeding season. Initially, we intended to include as many urban corvid species as possible. Our analysis focused solely on Magpies for reasons detailed in section 4.1. This paper was funded by the Internal Grant Competition (IGA) of the Faculty of Environmental Sciences at the Czech University of Life Sciences Prague (IGA 2022B0001).

My co-authored publications are not limited to specific taxa and encompass entire urban avian communities. The third paper of this thesis (see Annex III: Research III) continues on the theme of FID and antipredator behavior. Here, we explore the role of refuge availability, proximity, and type on the FID and the DF of urban birds in five cities in four European countries during the breeding seasons of 2021 and 2022.

The last paper in this thesis (see Annex IV: Research IV) belongs to the same large project as Research I, but it involves all the observed bird species, not just corvids. In this study, we investigate the potential of two Landsat-derived vegetation indices (NDVI and EVI) to act as proxies of various avian diversity indices in European cities.

4.1- Distribution of corvids in urban environments

Urban ecological studies focusing on corvids can highlight their advantages and disadvantages, identify factors promoting their presence, and inform measures to control their populations and mitigate their negative impacts (Benmazouz et al., 2021; Marzluff & Neatherlin, 2006).

In Research I (see Annex I) and Research IV (see Annex IV), which are part of the GACR project, fieldwork was conducted during the breeding season of 2018 by expert ornithologists

in several European cities. A single visit point count method was employed. Around 100 point counts spread evenly along a gradient of urbanization were randomly selected in each city. Each point was visited once for five minutes, during which all bird species heard singing or seen within a 50-meter radius were recorded, along with their abundance. Additional environmental factors were noted, including land use/land cover within the 50-meter point count radius, the number of people, cats, and dogs passing by in five minutes, and the average number of building floors. For more information on data collection, see Annex I (Section 2. "Materials and Methods") and Annex IV (Section "Methods").

For Research I, we used the subset of data concerning corvid species' presence and abundance, which allowed us to identify the corvid species present in European urban areas, along with their abundance and distribution.

4.1.1- The Western Jackdaw, the most abundant corvid:

Figure 1. A Western Jackdaw (*Corvus monedula*). Photo from Wikipedia:
https://en.wikipedia.org/wiki/western_jackdaw

Our results indicate that the Western Jackdaw (*Corvus monedula;* hereafter, "Jackdaw") is the most abundant corvid in the surveyed European cities. Generally sedentary in Europe, except in the north, where it is a short-distance migrant, the Jackdaw is omnivorous, monogamous, and gregarious (Svensson et al., 2010). It nests in cavities found in deciduous trees, mountains, sea cliffs, and buildings (Božič, 2016; Salvati, 2002; Svensson et al., 2010).

Despite being the most abundant corvid, the Jackdaw was not observed in Athens, Budapest, and Madrid. Around Madrid, Jackdaws may still be nesting within their natural habitats in

cliffs. Jackdaw density is declining sharply in Spain compared to the rest of Europe (Blanco et al., 2014, 2022). Until the early 21st century, Jackdaw pairs foraged in waste dumps around Madrid, especially outside the breeding season (Blanco et al., 2022). Today, however, such a sight might be rare, possibly due to the rubbish's low nutritional quality and high toxin levels, which may have affected their population over time (Meyrier et al., 2017; Plaza & Lambertucci, 2017). Additionally, Jackdaws face high persecution in and around Madrid, contributing to their reduced population and avoidance of the area (Blanco et al., 2019, 2022). Similar factors might explain their absence in Athens and Budapest, although we could not identify studies addressing these issues.

Jackdaws are at risk of population decline due to reduced nesting sites within urban areas. They are cavity nesters who rely on cavities in old buildings and are therefore threatened by renovations and modernization (Božič, 2016; Grünwald et al., 2024; Salvati, 2002). Thus, even the most abundant corvid in our study was impacted by varying factors that limited their presence in certain cities. For that reason, long-term population monitoring is important, especially when species are classified as "Least Concern" and may face increased risk of persecution due to assumptions of overpopulation (Blanco et al., 2022).

4.1.2- The Eurasian Magpie, the most spread corvid:

Figure 2. A Eurasian Magpie (*Pica pica*).
Photo from Wikipedia: https://en.wikipedia.org/wiki/Magpie

The Magpie was the most widespread corvid detected across all the surveyed European cities. Like the Jackdaw, the Magpie is sedentary, omnivorous, occasionally gregarious, and usually found in farmlands and urban areas (Svensson et al., 2010). The species typically build their nests in tree crowns using roofed sticks (Svensson et al., 2010).

Magpies were heavily persecuted in the past in some European cities (i.e., in Finland up until the early 1970s). However, they quickly habituated to human presence once persecution ceased, becoming highly successful in colonizing urban areas (Jokimäki et al., 2017, 2022). A recent study reported an exponential increase in the species' range in southern Spain, mainly attributed to urban areas (De la Cruz et al., 2024). Magpies are highly adaptable and were observed to modify their behaviors in urban areas to increase their survival. In urban areas, Magpies tend to nest higher in trees and more often in coniferous trees (as deciduous trees are exposed at the start of the spring), and these adaptations allow them to decrease predation risks from mesopredators (i.e., cats) and Carrion/Hooded Crows (*Corvus corone corone*/*Corvus corone cornix*) and disturbance from humans (Ciebiera et al., 2021; Jokimäki et al., 2017; Šálek, 2020). However, these nesting behaviors may also reflect the difference in the availability of tree types and heights between dense city centers and suburban areas (Dupak & Telizhenko, 2023). Compared to Magpies, Hooded Crows show more selectivity in their preferred tree species and nesting heights (Dupak & Telizhenko, 2023). Still, this would show Magpies' adaptability and capacity to exploit the available trees in cities for nesting, explaining their extensive spread and presence in all surveyed cities.

4.1.3- The Hooded/Carrion Crow:

Figure 3. A Carrion Crow (*Corvus corone corone*; left) and Hooded Crow (*Corvus corone cornix*; right). Photos from Wikipedia: https://en.wikipedia.org/wiki/Carrion_crow; https://en.wikipedia.org/wiki/Hooded_crow

In our study, we merged observations of The Hooded Crow (*Corvus corone cornix*) and the Carrion Crow (*Corvus corone corone*) and considered them as one species (hereafter "Crow") (see Annex I, section 2.4. "Classification of the Carrion Crow and the Hooded Crow" for more details). The Crow is a sedentary omnivore and a short-distance migrant in northern Europe (Svensson et al., 2010). The species breeds in open woodlands, urban areas, and within tree patches of farmlands, nesting in well-concealed open stick nests in tree crowns (Svensson et al., 2010).

The Crow was common, spread, and observed in all cities except the Spanish ones (Granada, Madrid, and Toledo). It is possible that Crows, like Jackdaws, still face persecution in Spain, deterring them from urban areas.

Our study, conducted during the breeding season, found that the three most common corvids in European cities are the Magpie, the Jackdaw, and the Crow, which is consistent with findings from a study conducted in Finland during the winter season (Jokimäki et al., 2022).

4.1.4- Less common corvids: the Rook and the Eurasian Jay:

Figure 4. A Rook (*Corvus frugilegus*; left) and a Eurasian Jay (*Garrulus glandarius*; right). Photos from Wikipedia: https://en.wikipedia.org/wiki/Rook_(bird); https://en.wikipedia.org/wiki/Jay

The Eurasian Jay (*Garrulus glandarius*, hereafter "Jay") was observed in half of the cities surveyed (Athens, Budapest, Groningen, Ioannina, Poitiers, Poznan, Prague, and Zielona Góra). The Jay is an omnivore, mostly resident species that nests primarily in trees in diverse types of woodlands (Svensson et al., 2010).

The Rook (*Corvus frugilegus*, hereafter "Rook") was less spread and abundant, only being present in five cities (Groningen, Poitiers, Poznan, Prague, and Tartu). The Rook is omnivorous (but feeds mainly on insects and earthworms), gregarious, and resident species (but migrant in northern Europe; Svensson et al., 2010). Colonies nest primarily in agricultural areas, making loose stick nests in tree patches (Svensson et al., 2010).

In general, the Rook population in Europe is declining. The species is listed as vulnerable on the European Red List of Species, potentially due to legal persecution and nest site destruction (Krüger et al., 2020; BirdLife International, 2021).

The Jay, a seed specialist, is expected to be less common in urban areas compared to the other generalist corvids in the study (Jokimäki et al., 2022). Both the Rook and the Jay were demonstrated to utilize urban areas more often during the winter season to benefit from the milder winters and abundant food while preferring more natural areas with higher quality food during the breeding season (Jadczyk & Drzeniecka-Osiadacz, 2013; Matsyura et al., 2016; Obukhova, 2018; Zimaroyeva et al., 2016).

4.1.5- The least common corvid in the European cities surveyed:

Figure 5. A Common Raven (*Corvus corax*). Photo from Wikipedia:
https://en.wikipedia.org/wiki/Common_raven

The Common Raven (*Corvus corax*, hereafter "Raven") was the least observed corvid in our study, with only two sightings across all surveyed cities. Consequently, these observations were excluded from the analysis. The Raven is a sedentary, omnivorous, monogamous species and the largest passerine (Svensson et al., 2010). The species breeds in uplands, deserted woods, and cliffs, building stick nests in trees or cliff ledges (Svensson et al., 2010). Although the Raven may be urbanized in some European cities, the species may avoid anthropogenic areas because of long-term persecution and is still primarily shy and wary (Jokimäki et al., 2022; Svensson et al., 2010).

Our study did not observe other corvid species that may be present in Europe. We documented which corvids are seen in European cities during the breeding season, identifying the most widespread species and those more rarely sighted.

4.1.6- Focusing on Magpies in Research II:

For my second first-authored article (see Annex II: Research II), we initially intended to include as many of the urban corvid species observed in European cities as possible. However, the scale of this study was much smaller as it was conducted solely in Prague, Czech Republic. In addition, this paper did not include all observed corvids as it focuses on the impacts of ambient noise on the antipredator behavior (measured by FID), which required sampling only distracted individuals on the ground. The Magpie was the only species we encountered frequently and

across a gradient of urban noise. Although Jackdaws were also common, they mainly were aggregated in two small parks in the city center where noise levels were consistently elevated due to proximity to the roads and metro stations. Research I showed that jackdaws are quite abundant but less spread than Magpies. Furthermore, we proved the tendency for Jackdaws to be observed in highly dense urban areas. Therefore, encountering them in areas with consistently elevated noise levels was not surprising. For that reason, we had to exclude Jackdaws from the analyses.

As for the other species, we encountered only around 7 Rook and 7 Jay individuals, so we had to exclude both (Sol et al., 2018). Both species were less common than Magpies and Jackdaws in the previous study and, as shown by the literature, are more likely to utilize urban areas in the winter (Jadczyk & Drzeniecka-Osiadacz, 2013; Matsyura et al., 2016; Obukhova, 2018; Zimaroyeva et al., 2016). Many Jays were observed in trees rather than foraging on the ground, indicating they may be shyer and warier than other corvids. We avoided approaching birds perched in trees to reduce confounding variables, as sheltering in trees may provide a sense of security to birds, as shown in Research III (see Annex III and section 4.4). Consequently, our study was limited only to Magpies.

4.2- Habitat selection of corvids and overlap

Returning to Research I, we aimed to assess the corvids' habitat preferences and their habitat and spatial overlap. Along with the variables collected in the field, models were run to estimate noise pollution levels around the point counts. Information regarding light pollution levels was downloaded from the web (https://www.lightpollutionmap.info). For detailed information on noise and light pollution estimates, see Annex I (Section "2.3. Variables Studied in Terms of Corvid Habitat Selection"). Generalized Linear Mixed Models (hereafter "GLMM") were run to assess each corvid species' habitat preferences. Spatial overlap was tested using a spatial mismatch analysis through a Mantel test (Mantel, 1967). Probabilistic niche regions (defined as a 95% probability region in multivariate space) for each species were estimated according to the land cover/land-use composition of point counts where the species were observed (Swanson et al., 2015). Then, a directional probabilistic niche overlap of each pair of corvid species was deduced (Swanson et al., 2015). For a detailed description of the statistical analyses, see Annex I (Section: "2.5. Statistical Analyses").

Three corvids (the Magpie, Crow, and Rook) were positively correlated to open habitats (grass and/or bare soil cover). Food availability is one of the main factors determining the habitat selection of corvids in urban areas (Matsubara, 2003; Preininger et al., 2019; Yoda, 2019). Although the species may utilize anthropogenic food sources in urban areas, during the breeding season, they are more likely to depend on high-nutritional foods such as insects, snails, and earthworms to provide their juveniles with nutrient-dense food (Díaz, 1996; Meyrier et al., 2017; Preininger et al., 2019; Seed et al., 2009). Pellet analyses of urban Magpies in Spain showed that the species' diet mainly consisted of snails, insects, and seeds and not so much of birds or anthropogenic foods (De la Cruz et al., 2024). The corvids are more likely to encounter these resources in open habitats, such as grass and bare soil. These results are congruent with other research, in and out of urban regions, where corvids were positively linked to open spaces, such as grasslands (Mason & Macdonald, 2004; Szala et al., 2020; Tzortzakaki et al., 2018; Waite, 1984b; Zimaroyeva et al., 2016).

Meanwhile, the Jay was positively linked to tree cover. Compared to this study's other corvid species Jay's diet is more specialist and dependent on seeds rather than animal sources (Jokimäki et al., 2022; Pesendorfer et al., 2016). Jays are possibly the main factor behind the seed dispersal of acron (*Quercus* spp.) and have developed a mutualist relationship with oak species (Bossema, 1979; Clayton et al., 1996; Kurek et al., 2018; Morán-López et al., 2015; Perea et al., 2011; Pons & Pausas, 2008). The species practices seed caching behavior in shallow ground, which favors seed germination and long-distance dispersal of oak seeds (Pesendorfer et al., 2016). The birds selectively choose which acorn seeds to cache, thus influencing the oak population compositions and potentially affecting the whole ecosystem dynamics, earning Jays the title of ecosystem engineers (Mitrus & Szabo, 2020; Pesendorfer et al., 2016). Jays select uninfected and nondamaged acorns of a certain size (suitable for swallowing) and potentially more nutritiously dense (Bossema, 1979; Mitrus & Szabo, 2020; Pons & Pausas, 2007). Therefore, Jays provide valuable ecosystem services that may aid habitat restoration of forests after disturbance (Pesendorfer et al., 2016). Jays are typical forest dwellers associated with tree cover within and outside urban areas (Matsyura et al., 2016; Pons & Pausas, 2008; Tzortzakaki et al., 2018).

On the other hand, the Jackdaw was negatively associated with the bare soil cover. The built cover was removed from our models for being correlated to the grass and bare soil covers, so we believe this result may reflect the decrease in built cover rather than the actual bare soil cover. Other studies have found that Jackdaws were linked to higher urban densities because

they prefer these areas for nesting (cavity nesters that tend to nest within building holes; Liordos et al., 2021; Salvati, 2002; Zmihorski et al., 2010). Although studies have shown that they need a mix of open areas along with rocky/built-up areas, it may seem that the impact of the built cover is stronger for their habitat selection, meaning they need areas with high building covers and smaller open habitats where they can forage (Salvati, 2002).

The preferred urban habitats of each corvid species seemed to reflect their habitat selection in natural environments and were influenced by their nesting site preferences (i.e., Jackdaw) and their diets (other corvids).

All five corvid species had high levels of habitat overlap. The two species with the least overlap (although still high) were the Jackdaw and Jay. These results were expected as the Jackdaw prefers areas with higher build cover while the Jay prefers forested regions. The Rook had the smaller niche, almost fully embedded in the ones of the other species. We expect that the Rooks would have larger niches in the winter season, where they are more likely to resort to urban environments for warmer temperatures and more abundant food (Zmihorski et al., 2010). Despite having specific preferences, the high niche overlap between corvid species shows that these species are generalists that can tolerate various environments despite preferences.

Although the species overlapped highly in their preferences, their distributions were only congruent with those sharing similar habitat features. The three species that selected open habitats (Magpies, Rooks, and Crows) were likelier to be seen simultaneously than expected by chance. Additionally, the presence of the Jay was positively related to that of Magpies and Crows. Since Jays prefer habitats with increased tree cover, while the other two species prefer open habitats, they may co-occur in urban parks where both habitats are abundant. The Jay's presence was not significantly associated with the Rooks, but this could be due to the low abundance of both species in the study. The Jackdaw's occurrence was not significantly related to any other species. Unlike the different species, Jackdaws seem to prefer densely built-up areas with abundant nesting sites. Jackdaws were shown to defend their nesting sites aggressively and tend to dominate other species (Roell, 1978). However, if that were the case here, we'd expect a negative association with the distribution of the species. It is more likely, therefore, that the different habitat preferences have caused these results.

Since none of the species' occurrence negatively affected the presence of another and species with similar habitat preferences were often co-occurring, we can conclude that competition is not negatively impacting these species and that they are not actively avoiding areas occupied

by other species. Several factors may explain the lack of negative spatial associations among the species, particularly those with similar habitat preferences. First, disturbed environments, such as urban areas, may facilitate the co-existence of sympatric species by providing ample resources and opportunities for habitation (Moi et al., 2020). Second, these corvid species have only recently begun to colonize urban areas and may not have reached the environment's carrying capacity yet (Tobias et al., 2020). Lastly, these species may be able to share the same habitats due to having separation in their niches at other scales, such as food type, feeding behavior, and nesting site (Dupak & Telizhenko, 2023; Kulemeyer et al., 2009; Matsubara, 2003; Waite, 1984a).

We showed that urban habitat preferences of corvids often mirror their preferences in natural environments and are largely impacted by their dietary choices and nesting sites. Despite having particular preferences, we observed a large overlap in their niches, suggesting that these species are generalists who can tolerate different environments beyond their ideal habitats. Species with similar preferences showed congruent distributions, demonstrating that competition does not adversely affect their habitat use in urban regions.

Future studies should consider other areas of niche overlap in corvids, including their nesting site and food resource preferences. These may show more partitioning than the simple habitats we studied. Behavioral studies on interspecific relationships between corvids would provide more insight into their co-existence (Waite, 1984a). Finally, studies can take a broader range of environmental gradients extending to rural, agricultural, and natural environments where these species are often sighted.

4.3- FID and noise

Research I (see Annex I) examined the habitat selection and overlap of corvids in urban areas. In contrast, Research II (see Annex II) explores some of the behavioral aspects of urban ecology, focusing on the impacts of urban noise pollution on the antipredator behavior of Magpies. The decision to focus solely on Magpies is explained in section 4.1.6.

Studies suggested that urban noise might affect the antipredator behavior in two ways: by distracting the individual or masking predator cues (thus reducing AD) or by causing the animal to become more vigilant to compensate for reduced auditory detection (thus increasing AD, which would entail additional energy costs; (Barber et al., 2010; Chan, David Stahlman, et al., 2010; Chan, Giraldo-Perez, et al., 2010; Evans et al., 2018; Kern & Radford, 2016; Meillère et

al., 2015; Shannon et al., 2016; Zhou et al., 2019). Previous studies on the impacts of noise on the antipredator behavior of birds did not include AD and used FID as a proxy for predator detection, claiming that AD and FID are strongly correlated (Gravolin et al., 2014; Meillère et al., 2015; Petrelli et al., 2017). We hypothesized that the impact of noise on FID may not reflect the same effects on AD.

We assumed that noise could reduce AD due to distraction and impaired hearing while potentially increasing FID as birds may react more quickly to threats to compensate for the reduced AD. So, although AD and FID are highly correlated, we hypothesized that some factors, such as noise, may reduce the correlation between these two measures, affecting birds' attention and escape responses in distinct ways. For instance, Novĉić (2023) found that crows engaged in foraging activities delayed flight after threat detection. Therefore, the speed of response post-predator detection offers additional insight into the antipredator behavior.

During the 2022 breeding season, we used standardized FID collection methods in the urban parks around Prague, Czech Republic. We approached distracted Magpies at a constant speed, recording the SD, AD, and FID (see Figure 6). We also noted the birds' age and measured noise levels with an environmental multimeter (13/464/0 from Brannan). Noise levels were measured immediately after FID collection to ensure accuracy, averaging the maximum and minimum levels recorded over one minute (see Annex II, section "2.1 Study area and field data collection" for more details). Two GLMMs were run with the SD, noise levels, and age of the individual as the predictors and the site as the random factor to control for variability among different parks. The first model used AD as the response variable, and the second used FID/AD (indicating escape speed post-detection; see Annex II, section "2.2 statistical analyses" for more details).
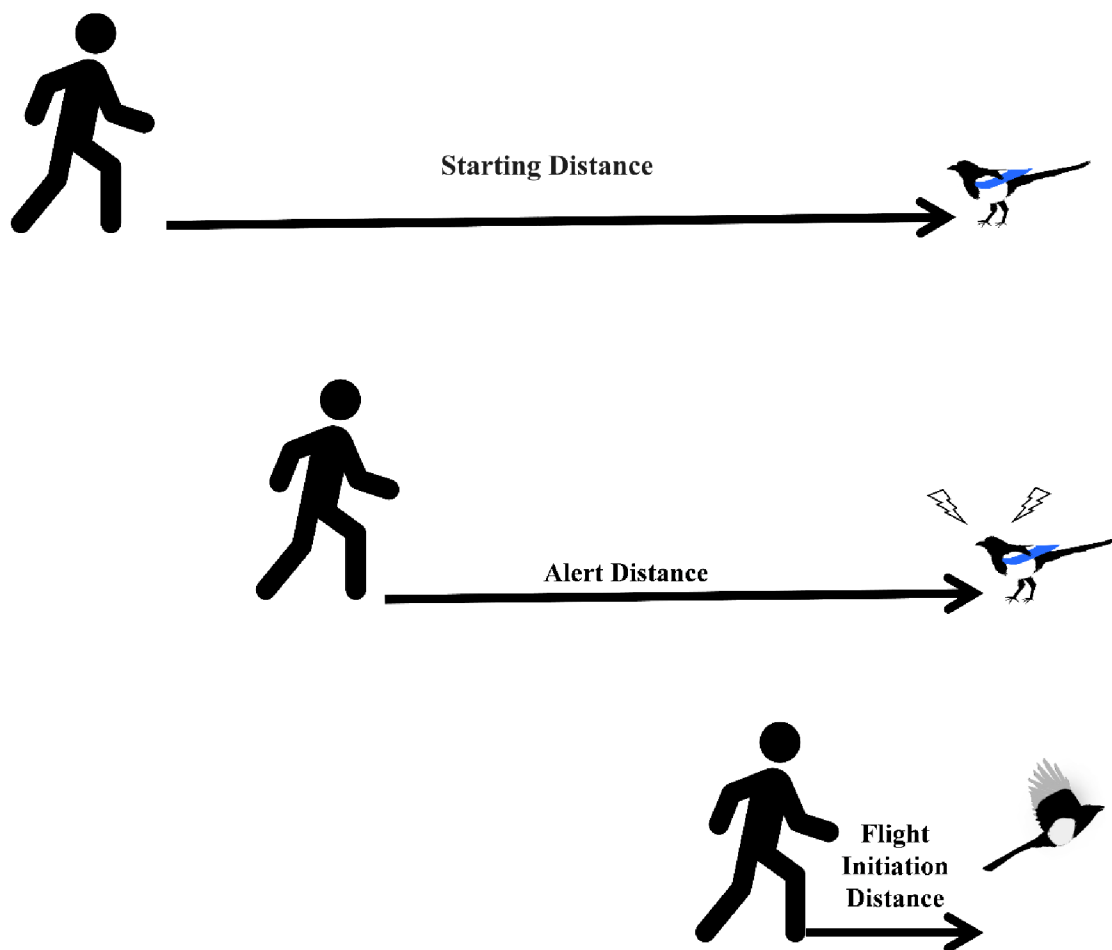
Figure 6. The Starting Distance (SD), Alert Distance (AD), and Flight Initiation Distance (FID) collection for Magpies.

The models included data from 167 individuals (138 adults and 29 juveniles) across 11 sites (see Annex II, section "3. Results" for detailed results). Contrary to our hypotheses, we found no effect of noise on the AD of Magpies, and to our surprise, we found that the birds delayed their response after detecting a threat in noisier environments.

A concurrent study found that Australian Magpies (*Gymnorhina tibicen dorsalis*) increase their vigilance due to noise pollution, leading the individuals to reduce their feeding rates and increase visual scans (Blackburn et al., 2024). Thus, increased vigilance may suffice to maintain consistent ADs despite noise (Tätte et al., 2019). Alternatively, some birds with wide visual fields might detect predators while foraging without relying heavily on auditory cues

and would, thus, not require increased vigilance at higher noise (Blumstein et al., 2004; Fernández-Juricic et al., 2004; Lima & Bednekoff, 1999). Future studies should look into more precise measures of predator detection, such as using telemetric eye trackers, to confirm better or refute the possible impact of noise on predator detection in Magpies (Yorzinski & Platt, 2014). Still, in our study, we did not find any effects of noise on the displayed alertness of the Magpies through AD (i.e., head-turning, looking at the approaching person, or agitation).

Contrary to our hypothesis, higher noise levels delayed the birds' escape after detecting a threat. Two potential theories may help explain these findings. First, while the noise did not distract the birds from detecting predators, it may have overwhelmed their cognitive processes, leading to slower decision-making and response execution. Tätte et al. (2019) observed that increased vigilance in urban environments results in longer danger assessment and escape times despite unaffected ADs. Those findings align with our results and suggest that distraction might impact other aspects of antipredator behavior beyond predator detection (Dukas, 2002). It also shows that increasing vigilance may help stabilize AD but not offset an effect on escape. Second, even if Magpies do not rely on auditory cues for threat detection (i.e., due to having wide visual fields), hearing predator cues can add to visual cues, causing multisensory integration and potentially leading to a quicker response (Munoz & Blumstein, 2012; Partan, 2017). Under higher noise levels, this effect may be diminished due to the masking of predator sounds. Future studies should investigate these two theories.

In this study, we showed that urban noise may slow down the reaction of Magpies without necessarily affecting their threat detection capacity. Nevertheless, it is crucial to remember our study's small scale and limited dataset. We also focused on one species, while different species may respond differently to urban noise (Petrelli et al., 2017). We suggest that future studies use other vigilance measures besides AD and FID to assess noise impacts on various aspects of antipredator behavior. Finally, Blackburn et al. (2024) found a combined effect of urban heat stress and noise. Therefore, studying the effect of noise pollution in combination with other stressors is necessary for the future.

4.4- FID and refuge

Remaining in the FID theme, Research III (see Annex III) investigates the role of refuge availability, type, and distance on the antipredator behavior of birds. In contrast to the previous

paper, this one is large-scale across five European cities in four different countries with 2900 FIDs of 85 bird species collected.

Research on the effects of refuge on birds has been lacking, particularly in urban regions. FID collection was conducted in five cities within four European countries during the breeding seasons of 2020 and 2021. Standard protocols were followed, similar to Research II. This paper sampled all observed terrestrial bird species (with a sample size ≥ 10). Other variables were collected: the flock size, level of urbanization (i.e., core vs. suburban), habitat type (i.e., cemetery, garden, park, or other urban areas), land-use composition (within 50 m around the collection point), SD, FID, distance to the nearest refuge considering these types (artificial, bush, or tree or patch of trees), DF to the shelter, and the kind of refuge used. See Annex III (Section 2.1 "Study area, flight initiation distance and refuge type") for a more detailed description of these parameters.

Pearson's chi-square test of independence was performed to explore the association between the availability of the nearest and the used refuge (i.e., artificial, bush, or tree). Then, we used two sets of multi-predictor Bayesian phylogenetically informed regression models to test associations between FID (response variable) and various predictors. The predictors in the first model were the mean distance of the nearest available refuge of each type, SD, flock size, land use composition, level of urbanization, and habitat type. In the second model, the predictors were DF, type of used refuge, SD, flock size, land use composition, level of urbanization, and habitat type. See Annex II (Section "2.2. Statistical analyses"; Section "3. Results") for the detailed statistical analysis.

Trees were the most common and closest available refuge, and they were used more frequently as refuge despite the relative availability of other types. Thus, birds were willing to flee longer distances and invest more energy to seek shelter in trees even though different types of refuges may be closer. On the other hand, bushes and artificial structures were underused relative to their availability, meaning that birds likely perceive them as less secure.

Our results demonstrate that the birds' FIDs were positively related to the distance to the nearest potential refuge, supporting the hypothesis that perceived predation risk increases with the safety distance, leading to an earlier escape (Cooper & Frederick, 2007; Ydenberg & Dill, 1986).

Birds fled farther when sheltered in artificial structures and trees than bushes or ground landings. Birds may be willing to travel longer distances to trees followed by artificial

structures (such as street lamps or buildings) because they are higher and out of reach of the human approaching.

FID and the DF to the refuge were positively correlated. Thus, the distance to safety impacts the risk assessment. These results also suggest that fearfulness is a consistent personality trait and can be demonstrated homogenously during predatory encounters (W. E. Cooper & Wilson, 2007; Stankowich & Coss, 2007). Thus, fearful individuals who escape earlier will escape to farther shelters to avoid being caught.

This study demonstrates that refuge proximity, availability, and type influence antipredator behavior in urban birds, highlighting the role of trees as preferred safe-havens. Future studies should investigate the role of refuge type, availability, and proximity on different taxa in various regions, seasons, and habitats (i.e., various types of natural and anthropogenically altered environments). Lastly, the associations between the refuge and antipredator behavior may be age and species-specific, which requires further investigation (Petelle et al., 2013).

4.5- Remote sensing tools to survey diversity

Previous studies have shown that remote sensing vegetation indices such as the NDVI and EVI are reliable, accessible, and cost-effective tools for monitoring biodiversity in urban areas (Bino et al., 2008; Callaghan et al., 2020; Leveau, 2019; Leveau et al., 2018). These studies, however, have primarily focused on a few diversity indices, mainly species richness, and have been confined to single-city analyses. Although avian richness may increase in urban areas, this often occurs at the expense of native, endemic, and rare species, which are replaced by widespread generalists, leading to biotic homogenization (Blair, 1996; Devictor et al., 2007; McKinney, 2006; McKinney & Lockwood, 1999). Therefore, it is still unclear whether these vegetation indices can also relay more specific information regarding the community composition, potentially revealing homogenization in the avian assemblages. If so, these indices would provide accessible, reliable, fast, and affordable means to monitor avian compositions since field surveys may be expensive and time-consuming, particularly at large scales (Palmer, 1995).

In Research IV (see Annex IV), we examined NDVI and EVI's potential to act as surrogates for many avian facets of diversity. The fieldwork is the same as for Research I (see Annex I and section 4.1), but it involves all the bird species recorded in the bird counts, not just the

corvids (See Annex IV; section "Methods: Bird data collection" for the detailed fieldwork design).

Landsat 30-meter resolution EVI and NDVI values were extracted using Google Earth Engine. For each month, 2 to 3 images were obtained for each point count for 2017, 2018, and 2019 to ensure sufficient images after cloud cover filtering. At each pixel, the median EVI and NDVI were taken to reduce the effect of outliers. Then, the mean and standard deviation (hereafter "sd") were calculated for each point count (50 m radius) for the months of April, May, June, and July (to match the fieldwork period). In the end, using the monthly averages, the overall averages (EVI mean and NDVI mean) and sd (EVI sd and NDVI sd) were calculated, and these values were used in the analyses. See Annex IV, section "Methods: EVI and NDVI estimation" for the detailed calculations.

Next, the different facets of diversity describing taxonomic, functional (functional richness, functional evenness, and functional divergence), and phylogenetic diversity (phylogenetic diversity, phylogenetic species variability, and community evolutionary distinctiveness) were calculated based on the bird species present in each point count. We also calculated each community's urban tolerance mean by averaging the species' urban tolerance scores in the point counts. Finally, different bird specialization richness (diet, foraging behavior, foraging substrate, and habitat) scores were calculated for each community (at the distinct point counts). Each specialization richness score described the number of birds, scoring 1 for the specific specialization index in each community. See Annex IV (section "Methods: Facets of avian diversity assessment") for the detailed calculations.

GLMMs were run to check for associations between vegetation proxies and diversity facets. Each diversity facet was a response variable run separately with each predictor (NDVI mean, NDVI sd, EVI mean, and EVI sd). So, each model consisted of one diversity metric and one predictor. The city was used as a random factor. See Annex IV, section "Methods: Statistical analyses" for a detailed description of the statistical analyses.

The main results are summarized in Figure 7. below. See Annex IV (section "Results") for the full results.

Figure 7. Matrix representing the GLMM association types between avian diversity and community metrics and Landsat-derived indices. In the columns, the following response variables are: Bird species richness (BSR), Functional richness (FRic), Functional evenness (FEve), Functional divergence (FDiv), Community evolutionary distinctiveness (CED), Phylogenetic diversity (PD), Phylogenetic species variability (PSV), Urban Tolerance mean (UTM), Diet specialization richness (Diet), Foraging behavior specialization richness (Forb), Foraging substrate specialization richness (Forsub), Habitat specialization richness (Hab). In the rows, the following predictive variables are: EVI mean, EVI standard deviation (EVI sd), NDVI mean, and NDVI standard deviation (NDVI sd). Each predictive variable was assessed in separate models. Blue squares represent positive and significant associations. Red squares represent negative and significant associations. White squares represent non-significant associations. The selected best models—according to the lowest AIC and greater AICWt values—are indicated with a white dot.

Our large-scale study highlighted the capacity of NDVI and EVI to act as robust indicators of various facets of urban diversity. In particular, the NDVI mean was the best predictor of almost all indices studied. Previous studies have shown that vegetation indices can surrogate simple diversity metrics in urban areas (Bino et al., 2008; Leveau, 2019; Leveau et al., 2020). We have demonstrated that they are useful in identifying other aspects of community composition.

Specifically, higher vegetation cover was associated with most facets of diversity studied (except for functional divergence). Increased vegetation was linked positively to most of these indices except for phylogenetic species variability, urban tolerance, and foraging substrate specialism. Therefore, generally, areas with higher vegetation cover support more diverse communities that are functionally and phylogenetically richer, with more specialists and less urban tolerant species. Thus, a greater NDVI mean can help identify areas with lower avian biotic homogenization, which may not be inferred from simple assessments of species richness (Petchey & Gaston, 2006).

Our findings can have important conservational applications, showing that NDVI mean may be utilized to track community composition and changes. Therefore, we provide accessible and effective ways to monitor urban communities, enabling urban planning efforts to better conserve species assemblages in cities long-term (Matas-Granados et al., 2022).

Future studies should incorporate other remote sensing tools and indices that may enhance the precision of biodiversity monitoring or outperform NDVI as a biodiversity surrogate in urban areas (i.e., Benitez et al., 2024).

4.6- The role of urban forestry in supporting birds

In addition to the specific findings of each study, three of the discussed research directly highlight the value of urban forests, specifically trees. Research IV showed that areas with higher vegetation density supported communities with increased avian diversity at different levels, including many specialists, and showed less biotic homogenization. The promotion of specialists is also seen in Research I, where only the Jay, the most seed-specialist urbanized corvid, was associated with increased tree cover. Jays, serving as ecosystem engineers, provide essential ecosystem services such as seed dispersal (Mitrus & Szabo, 2020; Pesendorfer et al., 2016). In contrast, the more generalist corvid species preferred open areas or built environments. Research III demonstrated that proximity to trees provided urban birds with an increased sense of security and allowed them to delay their escape. Birds were also willing to travel longer distances to seek shelter in a tree. Those findings further stress the values of urban forests since proximity to urban trees reduced the birds' FIDs and DF to the shelter, allowing them to conserve energy and improve their foraging efficiency and overall fitness (W. E. Cooper & Frederick, 2007; Møller et al., 2013).

Although Research II does not directly support the positive role of trees, it highlights the negative impact of urban noise on the antipredator behavior of Magpies. Urban trees may mitigate or reduce this effect by acting as noise barriers (Ow & Ghosh, 2017).

Our research further emphasizes the importance of preserving and increasing urban tree covers and aligns with the extensive literature on the countless values of urban forestry and ecology. These findings are valuable for urban planning, wildlife management, and conservation strategies, highlighting the need to maintain elevated tree covers in urban areas to support various aspects of bird ecology.

CHAPTER 5. CONCLUSIONS

This thesis consists of four journal articles contributing to the quickly growing field of urban avian ecology. Two articles focus on corvids, a group of birds, many of whom managed to successfully colonize urban areas, while the other two have a larger scope that covers almost all of the urban avian community. One article focuses on the urban habitat selection and overlap (Research I), two others explore the antipredator behavior of urban birds (Research II and III), and the last article examines the possibility of using vegetation indices for large-scale avian diversity monitoring in urban areas (Research IV).

Firstly, we found that despite having some preferences, urban corvid species overlap highly in their habitat niches, which shows their generalistic nature. Those with similar preferences were more likely to co-occur together, showing low impacts of competition. Secondly, our results indicate that although urban noise may not affect Magpies' capacity to detect danger, it still delays their reaction and escape. Therefore, urban noise may impact the antipredator behavior of species in complex ways that still require further investigation. Thirdly, we also show the value of refuge availability, type, and proximity on the antipredator behavior, specifically trees, which are the favored bird shelter type. Birds with closer potential refuge, especially trees, escaped later and for shorter distances, saving energy and potentially improving their fitness. Lastly, we demonstrate that vegetation indices, particularly NDVI, may be cost-effective proxies for multifaceted avian diversity monitoring in urban areas. Thus, we provide accessible tools to guide conservation efforts in urban areas and promote healthier urban environments for species.

We acknowledge some of the specific limitations of our studies, which are elaborated in the previous section and the articles. Nevertheless, in general, all our fieldwork was conducted during the breeding season, which may differ from the winter season when the birds do not have to rear young and have reduced food sources (Møller et al., 2013; Novčić & Parača, 2022). Future studies should explore the impacts of urbanization on wintering bird communities. Although our research was limited to European countries and may not fully generalize to other regions with different climates, urban ecological studies in Europe can provide valuable insights for developing countries, helping them avoid some adverse impacts and adopt novel methods for study and preservation (Jokimäki et al., 2016). Still, studies in other regions, especially ones less represented by the literature, are heavily needed. Finally, our focus was solely on birds, which, although they serve as bioindicators, future research should address

other taxa and ecosystem dynamics (Benmazouz et al., 2021; Goodness et al., 2016; Morelli, Reif, et al., 2021).

Urbanization subjects avian communities to various challenges that uniquely impact different species. This thesis contributes to the extensive scientific field of urban ornithology, which seeks to uncover the relationship between birds and urbanization but still has endless questions to answer.

REFERENCES

Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology & Evolution*, *30*(2), 114–126.

Angel, S., Parent, J., Civco, D. L., Blei, A., & Potere, D. (2011). The dimensions of global urban expansion: Estimates and projections for all countries, 2000-2050. *Progress in Planning*, *75*(2), 53–107. https://doi.org/10.1016/j.progress.2011.04.001

Apfelbach, R., Parsons, M. H., Soini, H. A., & Novotny, M. V. (2015). Are single odorous components of a predator sufficient to elicit defensive behaviors in prey species? *Frontiers in Neuroscience*, *9*, 263. https://10.3389/fnins.2015.00263

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S. G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J. L., Kühn, I., Macgregor-Fors, I., McDonnell, M., Mörtberg, U., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society of London B - Biological Sciences*, *281*(1780), 20133330. https://doi.org/10.1098/rspb.2013.3330

Bae, S., Müller, J., Lee, D., Vierling, K. T., Vogeler, J. C., Vierling, L. A., Hudak, A. T., Latifi, H., & Thorn, S. (2018). Taxonomic, functional, and phylogenetic diversity of bird assemblages are oppositely associated to productivity and heterogeneity in temperate forests. *Remote Sensing of Environment*, *215*(May), 145–156. https://doi.org/10.1016/j.rse.2018.05.031

Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology and Evolution*, *25*(3), 180–189. https://doi.org/10.1016/j.tree.2009.08.002

Beckerman, A. P., Boots, M., & Gaston, K. J. (2007). Urban bird declines and the fear of cats. *Animal Conservation*, *10*(3), 320–325.

Benitez, C., Beland, M., Esaian, S., & Wood, E. M. (2024). High-resolution remotely sensed data characterizes indices of avifaunal habitat on private residential lands in a global metropolis. *Ecological Indicators*, *160*. https://doi.org/10.1016/j.ecolind.2024.111900

Benmazouz, I., Jokimäki, J., Lengyel, S., Juhász, L., Kaisanlahti-Jokimäki, M.-L., Kardos, G., Paládi, P., & Kövér, L. (2021). Corvids in Urban Environments: A Systematic Global Literature Review. *Animals*, 11(11), 3226. https://doi.org/10.3390/ani11113226

Berkhout, B. W., Budria, A., Thieltges, D. W., & Slabbekoorn, H. (2023). Anthropogenic noise pollution and wildlife diseases. *Trends in Parasitology*, *39*(3), 181–190.

Bermúdez-Cuamatzin, E., Ríos-Chelén, A. A., Gil, D., & Garcia, C. M. (2011). Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters*, *7*(1), 36–38.

Bino, G., Levin, N., Darawshi, S., Van Der Hal, N., Reich-Solomon, A., & Kark, S. (2008). Accurate prediction of bird species richness patterns in an urban environment using Landsat-derived NDVI and spectral unmixing. *International Journal of Remote Sensing*, *29*(13), 3675–3700. https://doi.org/10.1080/01431160701772534

Birkhead, T., Wimpenny, J., & Montgomerie, B. (2014). *Ten thousand birds: ornithology since Darwin*. Princeton University Press.

Blackburn, G., Ashton, B. J., & Ridley, A. R. (2024). Evidence that multiple anthropogenic stressors cumulatively affect foraging and vigilance in an urban-living bird. *Animal Behaviour*, *211*, 1–12. https://doi.org/10.1016/j.anbehav.2024.02.014

Blair, R. B. (1996). Land Use and Avian Species Diversity Along an Urban Gradient. *Ecological Applications*, *6*(2), 506–519.

Blanco, G., Cuevas, J. A., Frías, Ó., & del Barrio, J. L. G. (2019). A shot in the dark: Sport hunting of declining corvids promotes the inadvertent shooting of threatened red-billed choughs. *Journal for Nature Conservation*, *52*, 125739.

Blanco, G., Domínguez, L., Fernández, L., Martínez, F., González del Barrio, J. L., Frías, Ó., Cuevas, J. A., & Carrete, M. (2022). The Decline of Common Birds Exemplified by the Western Jackdaw Warns on Strong Environmental Degradation. *Conservation*, *2*(1), 80–96. https://doi.org/10.3390/conservation2010007

Blanco, G., Frías, Ó., Cuevas, J. A., González, J. L., & Martínez, F. (2014). Commonness of not-so-common birds: The need for baseline knowledge of actual population size for the validation of population size predictions. *Bird Study*, *61*(3), 351–360. https://doi.org/10.1080/00063657.2014.938018

Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: How life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, *71*(2), 389–399. https://doi.org/10.1016/j.anbehav.2005.05.010

Blumstein, D. T., Fernández-Juricic, E., LeDee, O., Larsen, E., Rodriguez-Prieto, I., & Zugmeyer, C. (2004). Avian risk assessment: effects of perching height and detectability. *Ethology*, *110*(4), 273-285.

Bonney, R., Cooper, C. B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K. V, & Shirk, J. (2009). Citizen science: a developing tool for expanding science knowledge and scientific literacy. *BioScience*, *59*(11), 977–984.

Bossema, I. (1979). Jays and oaks: an eco-ethological study of a symbiosis. *Behaviour*, *70*(1–2), 1–116.

Box, E. O., Holben, B. N., & Kalb, V. (1989). Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO_2 flux. *Vegetatio*, *80*(2), 71–89. https://doi.org/10.1007/BF00048034

Božič, L. (2016). Numbers, distribution and nest site characteristics of Jackdaw Corvus monedula in Slovenia and its conservation status. *Acrocephalus*, *37*(170–171), 123–150. https://doi.org/10.1515/acro-2016-0007

Brown, R. E., Brain, J. D., & Wang, N. (1997). The avian respiratory system: a unique model for studies of respiratory toxicosis and for monitoring air quality. *Environmental Health Perspectives*, *105*(2), 188–200.

Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology*, *73*(3), 434–440. https://doi.org/10.1111/j.0021-8790.2004.00814.x

Brumm, H., & Zollinger, S. A. (2013). Avian vocal production in noise. *Animal Communication and Noise*, 187–227.

Burns, F., Eaton, M. A., Burfield, I. J., Klvaňová, A., Šilarová, E., Staneva, A., & Gregory, R. D. (2021). Abundance decline in the avifauna of the European Union reveals cross-

continental similarities in biodiversity change. *Ecology and Evolution*, *11*(23), 16647–16660. https://doi.org/10.1002/ece3.8282

Buxton, R. T., Pearson, A. L., Lin, H. Y., Sanciangco, J. C., & Bennett, J. R. (2023). Exploring the relationship between bird diversity and anxiety and mood disorder hospitalisation rates. *Geo: Geography and Environment*, *10*(2). https://doi.org/10.1002/geo2.127

Callaghan, C. T., Major, R. E., Cornwell, W. K., Poore, A. G. B., Wilshire, J. H., & Lyons, M. B. (2020). A continental measure of urbanness predicts avian response to local urbanization. *Ecography*, *43*(4), 528–538.

Callaghan, C. T., Major, R. E., Wilshire, J. H., Martin, J. M., Kingsford, R. T., & Cornwell, W. K. (2019). Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos*, *128*(6), 845–858. https://doi.org/10.1111/oik.06158

Callaghan, C. T., Palacio, F. X., Benedetti, Y., Morelli, F., & Bowler, D. E. (2023). Large-scale spatial variability in urban tolerance of birds. *Journal of Animal Ecology*, *92*(2), 403–416. https://doi.org/10.1111/1365-2656.13862

Carrete, M., Martínez-Padilla, J., Rodríguez-Martínez, S., Rebolo-Ifrán, N., Palma, A., & Tella, J. L. (2016). Heritability of fear of humans in urban and rural populations of a bird species. *Scientific Reports*, *6*(1), 31060. https://doi.org/10.1038/srep31060

Carrete, M., & Tella, J. L. (2011). Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS ONE*, *6*(4). https://doi.org/10.1371/journal.pone.0018859

Catchpole, C. K., & Slater, P. J. B. (2003). *Bird song: biological themes and variations*. Cambridge university press.

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape and Urban Planning*, *74*(1), 46–69. https://doi.org/10.1016/j.landurbplan.2004.08.007

Chan, A. A. Y. H., David Stahlman, W., Garlick, D., Fast, C. D., Blumstein, D. T., & Blaisdell, A. P. (2010). Increased amplitude and duration of acoustic stimuli enhance distraction. *Animal Behaviour*, *80*(6), 1075–1079. https://doi.org/10.1016/j.anbehav.2010.09.025

Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S., & Blumstein, D. T. (2010). Anthropogenic noise affects risk assessment and attention: The distracted prey hypothesis. *Biology Letters*, *6*(4), 458–461. https://doi.org/10.1098/rsbl.2009.1081

Chen, X., Xie, W., & Shuai, L. (2020). Flush early and avoid the rush? It may depend on where you stand. *Ethology*, *126*(10), 987–992.

Chivian, E., & Bernstein, A. S. (2004). Embedded in nature: human health and biodiversity. *Environmental Health Perspectives*, *112*(1), A12–A13.

Ciebiera, O., Czechowski, P., Morelli, F., Piekarski, R., & Bocheński, M. (2021). Selection of Urbanized Areas by Magpie Pica pica in a Medium Size City in Poland. *Animals*, *11*(6), 1738. https://doi.org/10.3390/ani11061738

Clayton, N. S., Mellor, R., & Jackson, A. (1996). Seasonal patterns of food storing in the jay Garrulus glandarius. *Ibis*, *138*(2), 250–255.

Cocker, M. (2014). Birds and people. *Journal of Field Ornithology, 85*(3), 339-340. https://doi.org/10.1111/jofo.12073_1

Coelho, S., Ferreira, J., Rodrigues, V., & Lopes, M. (2022). Source apportionment of air pollution in European urban areas: Lessons from the ClairCity project. *Journal of Environmental Management*, *320*, 115899.

Collins, M. K., Magle, S. B., & Gallo, T. (2021). Global trends in urban wildlife ecology and conservation. *Biological Conservation*, *261*, 109236.

Conole, L. E., & Kirkpatrick, J. B. (2011). Functional and spatial differentiation of urban bird assemblages at the landscape scale. *Landscape and Urban Planning*, *100*(1–2), 11–23.

Cooper, W. E., Blumstein, D. T., & Blumstein, D. T. (2015). Escape behavior: importance, scope, and variables. *Escaping from Predators: An Integrative View of Escape Decisions*, 3–14.

Cooper, W. E., & Frederick, W. (2007). Optimal time to emerge from refuge. *Biological Journal of the Linnean Society*, *91*(3), 375–382.

Cooper, W. J., McShea, W. J., Forrester, T., & Luther, D. A. (2020). The value of local habitat heterogeneity and productivity when estimating avian species richness and species of concern. *Ecosphere*, *11*(5). https://doi.org/10.1002/ecs2.3107

Cooper, W. E., & Wilson, D. (2007). Beyond optimal escape theory: microhabitats as well as predation risk affect escape and refuge use by the phrynosomatid lizard Sceloporus virgatus. *Behaviour*, *144*(10), 1235–1254.

Cox, D. T. C., & Gaston, K. J. (2016). Urban bird feeding: Connecting people with nature. *PLoS ONE*, *11*(7). https://doi.org/10.1371/journal.pone.0158717

Cox, D. T., Shanahan, D. F., Hudson, H. L., Plummer, K. E., Siriwardena, G. M., Fuller, R. A., ... & Gaston, K. J. (2017). Doses of neighborhood nature: the benefits for mental health of living with nature. *AIBS Bulletin*, *67*(2), 147-155.

Croci, S., Butet, A., & Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits? *Condor*, *110*(2), 223–240. https://doi.org/10.1525/cond.2008.8409

Czech, B., Krausman, P., & Devers, P. (2000). Economic associations among causes of species endangerment in the United States. *U. S. Fish and Wildlife Service*.

Da Silva, A., & Kempenaers, B. (2017). Singing from North to South: latitudinal variation in timing of dawn singing under natural and artificial light conditions. *Journal of Animal Ecology*, *86*(6), 1286–1297.

Da Silva, A., Valcu, M., & Kempenaers, B. (2015). Light pollution alters the phenology of dawn and dusk singing in common European songbirds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1667), 20140126.

Dale, S., Lifjeld, J. T., & Rowe, M. (2015). Commonness and ecology, but not bigger brains, predict urban living in birds. *BMC Ecology*, *15*(1), 1–14. https://doi.org/10.1186/s12898-015-0044-x

Dauphiné, N., & Cooper, R. J. (2009). Impacts of free-ranging domestic cats (Felis catus) on birds in the United States: a review of recent research with conservation and management recommendations. *Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics*, *205*.

D'couto, R. B. (2016). The Role of Birds in English Literature and Poetry. *International Journal of Science and Research, 5*(4), 1014-1015.

De la Cruz, A., Morales, A., Korneeva, Y., & Castro, M. (2024). Analysing citizen science data to address the demographic expansion of the Eurasian Magpie (Pica pica) in southern Spain. *Journal of Ornithology 165,* 805–813. https://doi.org/10.1007/s10336-024-02154-3

Del Hoyo, J., Del Hoyo, J., Elliott, A., & Sargatal, J. (1992). *Handbook of the birds of the world* (Vol. 1, Issue 8). Lynx Ed.

Devictor, V., Julliard, R., Couvet, D., Lee, A., & Jiguet, F. (2007). Functional homogenization effect of urbanization on bird communities. *Conservation Biology*, *21*(3), 741–751. https://doi.org/10.1111/j.1523-1739.2007.00671.x

Díaz, M. (1996). Food choice by seed-eating birds in relation to seed chemistry. *Comparative Biochemistry and Physiology Part A: Physiology*, *113*(3), 239–246.

Díaz, M., Grim, T., Markó, G., Morelli, F., Alamo, J. D. I., & Jokimäki, J. (2021). Effects of climate variation on bird escape distances modulate community responses to global change. *Scientific Reports*, *11*(1), 12826. https://doi.org/10.1038/s41598-021-92273-1

Díaz, M., Ramos, A., & Concepción, E. D. (2022). Changing urban bird diversity: how to manage adaptively our closest relation with wildlife. *Ecosistemas*, *31*(1), 2354-2354. https://doi.org/10.7818/ECOS.2354

Dickmeis, T. (2009). Glucocorticoids and the circadian clock. *Journal of Endocrinology*, *200*(1), 3.

Doherty, T. S., Dickman, C. R., Glen, A. S., Newsome, T. M., Nimmo, D. G., Ritchie, E. G., Vanak, A. T., & Wirsing, A. J. (2017). The global impacts of domestic dogs on threatened vertebrates. *Biological Conservation*, *210*, 56–59.

Dominoni, D., Quetting, M., & Partecke, J. (2013). Artificial light at night advances avian reproductive physiology. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1756), 20123017.

Donovan, T. M., & Thompson, F. R. (2001). Modeling the ecological trap hypothesis: A habitat and demographic analysis for migrant songbirds. *Ecological Applications*, *11*(3), 871–882. https://doi.org/10.1890/1051-0761(2001)011[0871:MTETHA]2.0.CO;2

Dorado-Correa, A. M., Rodríguez-Rocha, M., & Brumm, H. (2016). Anthropogenic noise, but not artificial light levels predicts song behaviour in an equatorial bird. *Royal Society Open Science*, *3*(7), 160231.

Ducatez, S., Sayol, F., Sol, D., & Lefebvre, L. (2018). Are urban vertebrates city specialists, artificial habitat exploiters, or environmental generalists? *Integrative and Comparative Biology*, *58*(5), 929–938. https://doi.org/10.1093/icb/icy101

Dukas, R. (2002). Behavioural and ecological consequences of limited attention. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1427), 1539-1547.

Dupak, V. S., & Telizhenko, V. S. (2023). Interactions between hooded crows (Corvus cornix) and Eurasian magpies (Pica pica) and their nesting site preferences in anthropogenic landscapes . *Écoscience*, *30*(3–4), 210–222. https://doi.org/10.1080/11956860.2023.2300758

European Commission. (2011). *Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the*

Committee of the Regions Youth Opportunities Initiative. European Commission Brussels, Belgium.

Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P. J., McDonald, R. I., Parnell, S., Schewenius, M., Sendstad, M., & Seto, K. C. (2013). *Urbanization, biodiversity and ecosystem services: challenges and opportunities: a global assessment*. Springer Nature.

Evans, J. C., Dall, S. R. X., & Kight, C. R. (2018). Effects of ambient noise on zebra finch vigilance and foraging efficiency. *PLoS ONE*, *13*(12). https://doi.org/10.1371/journal.pone.0209471

Ferenc, M., Sedláček, O., Fuchs, R., Dinetti, M., Fraissinet, M., & Storch, D. (2014). Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. *Global Ecology and Biogeography*, *23*(4), 479–489. https://doi.org/10.1111/geb.12130

Fernández-Juricic, E., Blumstein, D. T., Abrica, G., Manriquez, L., Adams, L. B., Adams, R., ... & Rodriguez-Prieto, I. (2006). Relationships of anti-predator escape and post-escape responses with body mass and morphology: a comparative avian study. *Evolutionary ecology research*, *8*(4), 731-752.

Fernández-Juricic, E., Erichsen, J. T., & Kacelnik, A. (2004). Visual perception and social foraging in birds. *Trends in Ecology & Evolution*, *19*(1), 25–31.

Fernández-Juricic, E., Jimenez, M. D., & Lucas, E. (2002). Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology*, *80*(7), 1212–1220. https://doi.org/10.1139/z02-104

Fernandez-Juricic, E., & Jokimäki, J. (2001). A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity & Conservation*, *10*, 2023–2043.

Figueiro, M. G., & Rea, M. S. (2010). The effects of red and blue lights on circadian variations in cortisol, alpha amylase, and melatonin. *International Journal of Endocrinology*, *, 2010(1), 829351.*

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., & Gibbs, H. K. (2005). Global consequences of land use. *Science*, *309*(5734), 570–574.

Francis, C. D., & Barber, J. R. (2013). A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment, 11*(6), 305-313.

Francis, C. D., Ortega, C. P., & Cruz, A. (2009). Noise Pollution Changes Avian Communities and Species Interactions. *Current Biology*, *19*(16), 1415–1419. https://doi.org/10.1016/j.cub.2009.06.052

Fuller, R. A., Irvine, K. N., Devine-Wright, P., Warren, P. H., & Gaston, K. J. (2007). Psychological benefits of greenspace increase with biodiversity. *Biology Letters*, *3*(4), 390–394.

Fusco, J., Walker, E., Papaïx, J., Debolini, M., Bondeau, A., & Barnagaud, J. Y. (2021). Land Use Changes Threaten Bird Taxonomic and Functional Diversity Across the Mediterranean Basin: A Spatial Analysis to Prioritize Monitoring for Conservation.

Frontiers in Ecology and Evolution, *9*(March), 1–15. https://doi.org/10.3389/fevo.2021.612356

Garcia-Porta, J., Sol, D., Pennell, M., Sayol, F., Kaliontzopoulou, A., & Botero, C. A. (2022). Niche expansion and adaptive divergence in the global radiation of crows and ravens. *Nature Communications*, *13*(1). https://doi.org/10.1038/s41467-022-29707-5

Gaston, K. J. (2022). Birds and ecosystem services. *Current Biology*, *32*(20), R1163-R1166.

Gauthreaux, S. A., Belser, C. G., Rich, C., & Longcore, T. (2006). Effects of artificial night lighting on migrating birds. *Ecological consequences of artificial night lighting*, 67-93. Island Press Washington, DC.

Gil, D., & Brumm, H. (Eds.). (2014). *Avian urban ecology.* Oxford University Press, USA.

Gnanapragasam, J. J., Ekanayake, K. B., Ranawana, K., Symonds, M. R. E., & Weston, M. A. (2021). Civil war is associated with longer escape distances among Sri Lankan birds. *The American Naturalist*, *198*(5), 653–659.

Godet, L., Gaüzere, P., Jiguet, F., & Devictor, V. (2015). Dissociating several forms of commonness in birds sheds new light on biotic homogenization. *Global Ecology and Biogeography*, *24*(4), 416–426. https://doi.org/10.1111/geb.12266

Goodness, J., Andersson, E., Anderson, P. M. L., & Elmqvist, T. (2016). Exploring the links between functional traits and cultural ecosystem services to enhance urban ecosystem management. *Ecological Indicators*, *70*, 597–605. https://doi.org/10.1016/j.ecolind.2016.02.031

Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S., & MacNeil, M. A. (2018). Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature*, *559*(7713), 250–253. https://doi.org/10.1038/s41586-018-0202-3

Gravolin, I., Key, M., & Lill, A. (2014). Boldness of urban Australian magpies and local traffic volume. *Avian Biology Research*, *7*(4), 244–250. https://doi.org/10.3184/175815514X14151981691872

Greenwell, C. N., Calver, M. C., & Loneragan, N. R. (2019). Cat gets its tern: A case study of predation on a threatened coastal seabird. *Animals*, *9*(7), 445.

Grunst, M. L., Grunst, A. S., Pinxten, R., & Eens, M. (2021). Variable and consistent traffic noise negatively affect the sleep behavior of a free-living songbird. *Science of the Total Environment*, *778*, 146338.

Grunst, M. L., Raap, T., Grunst, A. S., Pinxten, R., Parenteau, C., Angelier, F., & Eens, M. (2020). Early-life exposure to artificial light at night elevates physiological stress in free-living songbirds. *Environmental Pollution*, *259*, 113895. https://doi.org/10.1016/j.envpol.2019.113895

Grünwald, J., Hanzelka, J., Voříšek, P., & Reif, J. (2024). Long-term population trends of 48 urban bird species correspond between urban and rural areas. *IScience*, *27*(5), 109717. https://doi.org/10.1016/j.isci.2024.109717

Güneralp, B., Reba, M., Hales, B. U., Wentz, E. A., & Seto, K. C. (2020). Trends in urban land expansion, density, and land transitions from 1970 to 2010: A global synthesis. *Environmental Research Letters*, *15*(4), 044015.

Gwinner, E., & Brandstätter, R. (2001). Complex bird clocks. *Philosophical Transactions of the Royal Society of London. Series B*, *356*(1415), 1801.

Hager, S. B., Cosentino, B. J., Aguilar-Gómez, M. A., Anderson, M. L., Bakermans, M., Boves, T. J., Brandes, D., Butler, M. W., Butler, E. M., & Cagle, N. L. (2017). Continent-wide analysis of how urbanization affects bird-window collision mortality in North America. *Biological Conservation*, *212*, 209–215.

Hedin, M., Hahs, A. K., Mata, L., & Lee, K. (2022). Connecting biodiversity with mental health and wellbeing—A review of methods and disciplinary perspectives. *Frontiers in Ecology and Evolution*, *10*, 865727.

Heyman, E., Gunnarsson, B., & Dovydavicius, L. (2017). Management of urban nature and its impact on bird ecosystem services. *Ecology and conservation of birds in urban environments*, 465-488.

Hobi, M. L., Dubinin, M., Graham, C. H., Coops, N. C., Clayton, M. K., Pidgeon, A. M., & Radeloff, V. C. (2017). A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness. *Remote Sensing of Environment*, *195*, 142–152. https://doi.org/10.1016/j.rse.2017.04.018

Hollén, L. I., & Radford, A. N. (2009). The development of alarm call behaviour in mammals and birds. *Animal Behaviour*, *78*(4), 791–800. https://doi.org/10.1016/j.anbehav.2009.07.021

Holmes, T. L., Knight, R. L., Stegall, L., & Craig, G. R. (1993). Responses of wintering grassland raptors to human disturbance. *Wildlife Society Bulletin (1973-2006)*, *21*(4), 461–468.

Horton, K. G., Nilsson, C., Van Doren, B. M., La Sorte, F. A., Dokter, A. M., & Farnsworth, A. (2019). Bright lights in the big cities: migratory birds' exposure to artificial light. *Frontiers in Ecology and the Environment*, *17*(4), 209–214.

Hu, Y., & Cardoso, G. C. (2009). Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behavioral Ecology*, *20*(6), 1268–1273. https://doi.org/10.1093/beheco/arp131

Huete, A., Justice, C., & Van Leeuwen, W. (1999). MODIS vegetation index (MOD13). *Algorithm theoretical basis document*, *3*(213), 295-309.

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.*, *22*, 145–159.

Ibáñez-Álamo, J. D., Rubio, E., Benedetti, Y., & Morelli, F. (2017). Global loss of avian evolutionary uniqueness in urban areas. *Global Change Biology*, *23*(8), 2990–2998. https://doi.org/10.1111/gcb.13567

Isaksson, C. (2018). Impact of urbanization on birds. *Bird Species*. Springer, Cham. https://doi.org/10.1007/978-3-319-91689-7_13 *235*, 257.

Jadczyk, P., & Drzeniecka-Osiadacz, A. (2013). Feeding strategy of wintering rooks Corvus frugilegus L. in urban habitats. *Polish Journal of Ecology*, *61*(3), 587–596.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448.

Jokimäki, J., Kaisanlahti-Jokimäki, M. L., & Suhonen, J. (2022). Long-Term Winter Population Trends of Corvids in Relation to Urbanization and Climate at Northern Latitudes. *Animals*, *12*(14). https://doi.org/10.3390/ani12141820

Jokimäki, J., Suhonen, J., Jokimäki-Kaisanlahti, M. L., & Carbó-Ramírez, P. (2016). Effects of urbanization on breeding birds in European towns: Impacts of species traits. *Urban Ecosystems*, *19*(4), 1565–1577. https://doi.org/10.1007/s11252-014-0423-7

Jokimäki, J., Suhonen, J., Vuorisalo, T., Kövér, L., & Kaisanlahti-Jokimäki, M. L. (2017). Urbanization and nest-site selection of the Black-billed Magpie (Pica pica) populations in two Finnish cities: From a persecuted species to an urban exploiter. *Landscape and Urban Planning*, *157*, 577–585. https://doi.org/10.1016/j.landurbplan.2016.08.001

Julian, K. G., Eidson, M., Kipp, A. M., Weiss, E., Petersen, L. R., Miller, J. R., Hinten, S. R., & Marfin, A. A. (2002). Early season crow mortality as a sentinel for West Nile virus disease in humans, northeastern United States. *Vector Borne and Zoonotic Diseases*, *2*(3), 145–155.

Kark, S., Iwaniuk, A., Schalimtzek, A., & Banker, E. (2007). Living in the city: Can anyone become an "urban exploiter"? *Journal of Biogeography*, *34*(4), 638–651. https://doi.org/10.1111/j.1365-2699.2006.01638.x

Kempenaers, B., Borgström, P., Loës, P., Schlicht, E., & Valcu, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology*, *20*(19), 1735–1739.

Kent, E., Schwartz, A. L. W., & Perkins, S. E. (2021). Life in the fast lane: roadkill risk along an urban–rural gradient. *Journal of Urban Ecology*, *7*(1), juaa039.

Kern, J. M., & Radford, A. N. (2016). Anthropogenic noise disrupts use of vocal information about predation risk. *Environmental Pollution*, *218*, 988–995. https://doi.org/10.1016/j.envpol.2016.08.049

Konishi, M., Emlen, S. T., Ricklefs, R. E., & Wingfield, J. C. (1989). Contributions of Bird Studies to Biology. *Science*, *246*, 465. www.sciencemag.org

Kontsiotis, V. J., Valsamidis, E., & Liordos, V. (2019). Organization and differentiation of breeding bird communities across a forested to urban landscape. *Urban Forestry and Urban Greening*, *38*(January), 242–250. https://doi.org/10.1016/j.ufug.2019.01.007

Kosicki, J. Z. (2021). The impact of feral domestic cats on native bird populations. Predictive modelling approach on a country scale. *Ecological Complexity*, *48*. https://doi.org/10.1016/j.ecocom.2021.100964

Krüger, T., Heckenroth, H., Prior, N., Seitz, J., & Zang, H. (2020). Persecution and statutory protection have driven Rook Corvus frugilegus population dynamics over the past 120 years in NW-Germany. *Journal of Ornithology*, *161*, 569–584.

Kulemeyer, C., Asbahr, K., Gunz, P., Frahnert, S., & Bairlein, F. (2009). Functional morphology and integration of corvid skulls a 3D geometric morphometric approach. *Frontiers in Zoology*, *6*(1). https://doi.org/10.1186/1742-9994-6-2

Kurek, P., Dobrowolska, D., Wiatrowska, B., & Dylewski, L. (2018). What if Eurasian jay Garrulus glandarius would larder acorns instead of scatter them? *IForest-Biogeosciences and Forestry*, *11*(5), 685.

Lees, A. C., Haskell, L., Allinson, T., Bezeng, S. B., Burfield, I. J., Renjifo, L. M., Rosenberg, K. V, Viswanathan, A., & Butchart, S. H. M. (2022). State of the world's birds. *Annual Review of Environment and Resources, 47*(1), 231-260.

Lepczyk, C. A., Aronson, M. F. J., Evans, K. L., Goddard, M. A., Lerman, S. B., & Macivor, J. S. (2017). Biodiversity in the City: Fundamental Questions for Understanding the

Ecology of Urban Green Spaces for Biodiversity Conservation. *BioScience*, *67*(9), 799–807. https://doi.org/10.1093/biosci/bix079

Lepczyk, C. A., & Warren, P. S. (Eds.). (2012). *Urban bird ecology and conservation* (Vol. 45). Univ of California Press.

Leveau, L. M. (2019). Primary productivity and habitat diversity predict bird species richness and composition along urban-rural gradients of central Argentina. *Urban Forestry and Urban Greening*, *43*(April), 126349. https://doi.org/10.1016/j.ufug.2019.05.011

Leveau, L. M., Isla, F. I., & Bellocq, M. I. (2018). Predicting the seasonal dynamics of bird communities along an urban-rural gradient using NDVI. *Landscape and Urban Planning*, *177*(April), 103–113. https://doi.org/10.1016/j.landurbplan.2018.04.007

Leveau, L. M., Isla, F. I., & Isabel Bellocq, M. (2020). From town to town: Predicting the taxonomic, functional and phylogenetic diversity of birds using NDVI. *Ecological Indicators*, *119*(July), 106703. https://doi.org/10.1016/j.ecolind.2020.106703

Lima, S. L. (1993). Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *The Wilson Bulletin*, 1–47.

Lima, S. L., & Bednekoff, P. A. (1999). Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? *Animal Behaviour*, *58*(3), 537–543.

Liordos, V., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Valsamidis, E., & Kontsiotis, V. J. (2021). Niche analysis and conservation of bird species using urban core areas. *Sustainability*, *13*(11), 6327.

Liu, H. Q., & Huete, A. (1995). A feedback based modification of the NDVI to minimize canopy background and atmospheric noise. *IEEE Transactions on Geoscience and Remote Sensing*, *33*(2), 457–465.

Liu, Z., He, C., Zhou, Y., & Wu, J. (2014). How much of the world's land has been urbanized, really? A hierarchical framework for avoiding confusion. *Landscape Ecology*, *29*(5), 763–771. https://doi.org/10.1007/s10980-014-0034-y

Lizée, M. H., Mauffrey, J. F., Tatoni, T., & Deschamps-Cottin, M. (2011). Monitoring urban environments on the basis of biological traits. *Ecological Indicators*, *11*(2), 353–361. https://doi.org/10.1016/j.ecolind.2010.06.003

Lombard, E. (1911). Le signe de televation de la voix. *Annu. maladies oreille larynx nez pharynx*, *27*, 101-119.

Longcore, T., Rich, C., & Gauthreaux Jr, S. A. (2008). Height, guy wires, and steady-burning lights increase hazard of communication towers to nocturnal migrants: a review and meta-analysis. *The Auk*, *125*(2), 485–492.

Loss, S. R., Will, T., & Marra, P. P. (2013). The impact of free-ranging domestic cats on wildlife of the United States. *Nature Communications*, *4(1), 1-8*. https://doi.org/10.1038/ncomms2380

Luck, G. W., & Smallbone, L. T. (2010). Species diversity and urbanisation: patterns, drivers and implications. *Urban Ecology*, 88–119.

Madden, C. F., Arroyo, B., & Amar, A. (2015). A review of the impacts of corvids on bird productivity and abundance. *Ibis*, *157*(1), 1–16. https://doi.org/10.1111/ibi.12223

Mainwaring, M. C. (2015). The use of man-made structures as nesting sites by birds: A review of the costs and benefits. *Journal for Nature Conservation*, *25*, 17–22.

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Res.*, *27*, 209–220.

Marzluff, J. M. (2001). Worldwide urbanization and its effects on birds. *Avian Ecology and Conservation in an Urbanizing World*, 19–47.

Marzluff, J. M. (2017). A decadal review of urban ornithology and a prospectus for the future. *Ibis*, *159*(1), 1–13. https://doi.org/10.1111/ibi.12430

Marzluff, J. M., & Ewing, K. (2008). Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Urban Ecology: An International Perspective on the Interaction between Humans and Nature*, 739–755.

Marzluff, J. M., & Neatherlin, E. (2006). Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. *Biological Conservation*, *130*(2), 301–314. https://doi.org/10.1016/j.biocon.2005.12.026

Mason, C. F., & Macdonald, S. M. (2004). Distribution of foraging rooks, Corvus frugilegus, and rookeries in a landscape in eastern England dominated by winter cereals. *Folia Zoologica*, *53*(2), 179-188.

Matas-Granados, L., Pizarro, M., Cayuela, L., Domingo, D., Gómez, D., & García, M. B. (2022). Long-term monitoring of NDVI changes by remote sensing to assess the vulnerability of threatened plants. *Biological Conservation*, *265*. https://doi.org/10.1016/j.biocon.2021.109428

Matsubara, H. (2003). Comparative study of territoriality and habitat use in syntopic Jungle Crow (Corvus macrorhynchos) and Carrion Crow (C. corone). *Ornithological Science*, *2*(2), 103–111. https://doi.org/10.2326/osj.2.103

Matsushita, B., Yang, W., Chen, J., Onda, Y., & Qiu, G. (2007). Sensitivity of the Enhanced Vegetation Index (EVI) and Normalized Difference Vegetation Index (NDVI) to topographic effects: A case study in high-density cypress forest. *Sensors*, *7*(11), 2636–2651. https://doi.org/10.3390/s7112636

Matsyura, A. V., Zimaroyeva, A. A., & Jankowski, K. (2016). Spatial patterns of seasonal distribution of Corvidae (the case of urban habitats). *Biosystems Diversity*, *24*(2), 459–465. https://doi.org/10.15421/011662

McCloy, M. W. D., Andringa, R. K., Maness, T. J., Smith, J. A., & Grace, J. K. (2024). Promoting urban ecological resilience through the lens of avian biodiversity. *Frontiers in Ecology and Evolution*, *12*. https://doi.org/10.3389/fevo.2024.1302002

McDonald, R. I. (2008). Global urbanization: Can ecologists identify a sustainable way forward? *Frontiers in Ecology and the Environment*, *6*(2), 99–104. https://doi.org/10.1890/070038

McGranahan, G., & Satterthwaite, D. (2003). Urban centers: An assessment of sustainability. *Annual Review of Environment and Resources*, *28*, 243–274. https://doi.org/10.1146/annurev.energy.28.050302.105541

Mckinney, M. (2002). Urbanization, biodiversity, and conservation. *BioScience*, *52*, 883–890.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Meillère, A., Brischoux, F., & Angelier, F. (2015). Impact of chronic noise exposure on antipredator behavior: An experiment in breeding house sparrows. *Behavioral Ecology*, *26*(2), 569–577. https://doi.org/10.1093/beheco/aru232

Mekonen, S. (2017). Birds as biodiversity and environmental indicator. *Indicator*, *7*(21).

Meyrier, E., Jenni, L., Bötsch, Y., Strebel, S., Erne, B., & Tablado, Z. (2017). Happy to breed in the city? Urban food resources limit reproductive output in Western Jackdaws. *Ecology and Evolution*, *7*(5), 1363–1374.

Miller, J. R., & Hobbs, R. J. (2002). Conservation where people live and work. *Conservation Biology*, *16*(2), 330–337.

Mitrus, C., & Szabo, J. (2020). Foraging Eurasian jays (Garrulus glandarius) prefer oaks and acorns in Central Europe. *Ornis Hungarica*, *28*(1), 169–175. https://doi.org/10.2478/orhu-2020-0010

Moi, D. A., García-Ríos, R., Hong, Z., Daquila, B. V., & Mormul, R. P. (2020). Intermediate disturbance hypothesis in ecology: a literature review. *Annales Zoologici Fennici*, *57*(1–6), 67–78.

Møller, A. P. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*, *63*(1), 63–75. https://doi.org/10.1007/s00265-008-0636-y

Møller, A. P. (2009). Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, *159*(4), 849–858. https://doi.org/10.1007/s00442-008-1259-8

Møller, A. P. (2010). The fitness benefit of association with humans: Elevated success of birds breeding indoors. *Behavioral Ecology*, *21*(5), 913–918. https://doi.org/10.1093/beheco/arq079

Møller, A. P. (2021). Risk-taking behaviour as a central concept in evolutionary biology. *The World at Our Fingertips: A Multidisciplinary Exploration of Peripersonal Space*, 301–314. https://doi.org/10.1093/oso/9780198851738.003.0017

Møller, A. P., Grim, T., Ibáñez-Álamo, J. D., Markó, G., & Tryjanowski, P. (2013). Change in flight initiation distance between urban and rural habitats following a cold winter. *Behavioral Ecology*, *24*(5), 1211–1217. https://doi.org/10.1093/beheco/art054

Møller, A. P., Tryjanowski, P., Díaz, M., & Indykiewicz, P. (2015). Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behavioral Ecology, 26*(3), 861-865. https://doi.org/10.1093/beheco/arv024

Morán-López, T., Alonso, C. L., & Díaz, M. (2015). Landscape effects on jay foraging behavior decrease acorn dispersal services in dehesas. *Acta Oecologica*, *69*, 52–64.

Morelli, F., Benedetti, Y., Díaz, M., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Tätte, K., Markó, G., Jiang, Y., Tryjanowski, P., & Møller, A. P. (2019). Contagious fear: Escape behavior increases with flock size in European gregarious birds. *Ecology and Evolution*, *9*(10), 6096–6104. https://doi.org/10.1002/ece3.5193

Morelli, F., Benedetti, Y., Ibáñez-Álamo, J. D., Jokimäki, J., Mänd, R., Tryjanowski, P., & Møller, A. P. (2016). Evidence of evolutionary homogenization of bird communities in urban environments across Europe. *Global Ecology and Biogeography*, *25*, 1284–1293. https://doi.org/10.1111/geb.12486

Morelli, F., Benedetti, Y., Ibáñez-Álamo, J. D., Tryjanowski, P., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Suhonen, J., Díaz, M., Møller, A. P., & Moravec, D. (2021). Effects of urbanization on taxonomic, functional and phylogenetic avian diversity in Europe. *Science of the Total Environment*, *795*, 148874.

Morelli, F., Reif, J., Díaz, M., Tryjanowski, P., Ibáñez-Álamo, J. D., Suhonen, J., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Møller, A. P., Jerzak, L., Bussière, R., Mägi, M., Kominos, T., Galanaki, A., Bukas, N., Markó, G., Pruscini, F., Ciebiera, O., & Benedetti, Y. (2024). Dense city centers support less evolutionary unique bird communities than sparser urban areas. *IScience*, *27*(2). https://doi.org/10.1016/j.isci.2024.108945

Morelli, F., Reif, J., Díaz, M., Tryjanowski, P., Ibáñez-Álamo, J. D., Suhonen, J., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Pape Møller, A., Bussière, R., Mägi, M., Kominos, T., Galanaki, A., Bukas, N., Markó, G., Pruscini, F., Jerzak, L., Ciebiera, O., & Benedetti, Y. (2021). Top ten birds indicators of high environmental quality in European cities. *Ecological Indicators*, *133*. https://doi.org/10.1016/j.ecolind.2021.108397

Morelli, F., Tryjanowski, P., Ibáñez-Álamo, J. D., Díaz, M., Suhonen, J., Pape Møller, A., Prosek, J., Moravec, D., Bussière, R., Mägi, M., Kominos, T., Galanaki, A., Bukas, N., Markó, G., Pruscini, F., Reif, J., & Benedetti, Y. (2023). Effects of light and noise pollution on avian communities of European cities are correlated with the species' diet. *Scientific Reports*, *13*(1). https://doi.org/10.1038/s41598-023-31337-w

Munoz, N. E., & Blumstein, D. T. (2012). Multisensory perception in uncertain environments. *Behavioral Ecology*, *23*(3), 457–462. https://doi.org/10.1093/beheco/arr220

Navara, K. J., & Nelson, R. J. (2007). The dark side of light at night: physiological, epidemiological, and ecological consequences. *Journal of Pineal Research*, *43*(3), 215–224.

Neate-Clegg, M. H. C., Tonelli, B. A., Youngflesh, C., Wu, J. X., Montgomery, G. A., Şekercioğlu, Ç. H., & Tingley, M. W. (2023). Traits shaping urban tolerance in birds differ around the world. *Current Biology*, *33*(9), 1677-1688.e6. https://doi.org/10.1016/j.cub.2023.03.024

Nogales, M., Vidal, E., Medina, F. M., Bonnaud, E., Tershy, B. R., Campbell, K. J., & Zavaleta, E. S. (2013). Feral cats and biodiversity conservation: the urgent prioritization of island management. *Bioscience*, *63*(10), 804-810.

Novcić, I. (2023). Opposing effects of vigilance and foraging on escape behaviour in hooded crows. *Behaviour*, *127*. https://doi.org/10.1163/1568539X-bja10216

Novčić, I., & Parača, V. (2022). Seasonal differences in escape behaviour in the urban hooded crow, Corvus cornix. *Journal of Vertebrate Biology*, *71*(21066). https://doi.org/10.25225/jvb.21066

Obukhova, N. Y. (2018). Nesting Dynamics of Corvids (Corvidae) in the City of Moscow and Moscow Oblast. *Biology Bulletin*, *45*(9), 1096–1105. https://doi.org/10.1134/S1062359018090133

Oke, T. R. (1982). The energetic basis of the urban heat island. *Quarterly Journal of the Royal Meteorological Society*, *108*(455), 1–24.

Ow, L. F., & Ghosh, S. (2017). Urban cities and road traffic noise: Reduction through vegetation. *Applied Acoustics*, *120*, 15–20. https://doi.org/10.1016/j.apacoust.2017.01.007

Palmer, M. W. (1995). How should one count species? *Natural Areas Journal*, *15*, 124–135.

Partan, S. R. (2017). Multimodal shifts in noise: switching channels to communicate through rapid environmental change. *Animal Behaviour*, *124*, 325–337. https://doi.org/10.1016/j.anbehav.2016.08.003

Patankar, S., Jambhekar, R., Suryawanshi, K. R., & Nagendra, H. (2021). Which traits influence bird survival in the city? A review. *Land*, *10*(2), 1–23. https://doi.org/10.3390/land10020092

Pavisse, R., Vangeluwe, D., & Clergeau, P. (2019). Domestic cat predation on garden birds: An analysis from European ringing programmes. *Ardea*, *107*(1), 103–109.

Perea, R., San Miguel, A., & Gil, L. (2011). Flying vs. climbing: Factors controlling arboreal seed removal in oak–beech forests. *Forest Ecology and Management*, *262*(7), 1251–1257.

Pesendorfer, M. B., Sillett, T. S., Koenig, W. D., & Morrison, S. A. (2016). Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration. *Condor*, *118*(2), 215–237. https://doi.org/10.1650/CONDOR-15-125.1

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters*, *9*(6), 741–758.

Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A., & Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour*, *86*(6), 1147–1154. https://doi.org/10.1016/j.anbehav.2013.09.016

Petrelli, A. R., Levenhagen, M. J., Wardle, R., Barber, J. R., & Francis, C. D. (2017). First to flush: The effects of ambient noise on songbird flight initiation distances and implications for human experiences with nature. *Frontiers in Ecology and Evolution*, *5*(JUN). https://doi.org/10.3389/fevo.2017.00067

Pettorelli, N. (2013). *The normalized difference vegetation index*. Oxford University Press, USA.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, *20*(9), 503–510. https://doi.org/10.1016/j.tree.2005.05.011

Plaza, P. I., & Lambertucci, S. A. (2017). How are garbage dumps impacting vertebrate demography, health, and conservation? *Global Ecology and Conservation*, *12*, 9–20.

Pons, J., & Pausas, J. G. (2007). Not only size matters: Acorn selection by the European jay (Garrulus glandarius). *Acta Oecologica*, *31*(3), 353–360. https://doi.org/10.1016/j.actao.2007.01.004

Pons, J., & Pausas, J. G. (2008). Modelling jay (Garrulus glandarius) abundance and distribution for oak regeneration assessment in Mediterranean landscapes. *Forest Ecology and Management*, *256*(4), 578–584. https://doi.org/10.1016/j.foreco.2008.05.003

Preininger, D., Schoas, B., Kramer, D., & Boeckle, M. (2019). Waste disposal sites as all-you-can eat buffets for carrion crows (Corvus corone). *Animals*, *9*(5), 1–15. https://doi.org/10.3390/ani9050215

Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Lemmon, E. M., & Lemmon, A. R. (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, *526*(7574), 569–573.

Raap, T., Pinxten, R., & Eens, M. (2016). Artificial light at night disrupts sleep in female great tits (Parus major) during the nestling period, and is followed by a sleep rebound. *Environmental Pollution*, *215*, 125–134.

Ratcliffe, E., Gatersleben, B., & Sowden, P. T. (2013). Bird sounds and their contributions to perceived attention restoration and stress recovery. *Journal of Environmental Psychology*, *36*, 221–228. https://doi.org/10.1016/j.jenvp.2013.08.004

Rebolo-Ifrán, N., Zamora-Nasca, L., & Lambertucci, S. A. (2021). Cat and dog predation on birds: The importance of indirect predation after bird-window collisions. *Perspectives in Ecology and Conservation*, *19*(3), 293–299. https://doi.org/10.1016/j.pecon.2021.05.003

Reif, J., Prylová, K., Šizling, L., Vermouzek, Z., & Bejček, V. (2013). Changes in bird community composition in the Czech Republic from 1982 to 2004: increasing biotic homogenization, impacts of warming climate, but no trend in species richness. *Journal of Ornithology*, *154*(August), 359–370. https://doi.org/10.1007/s10336-012-0900-9

Ríos-Chelén, A. A., Quirós-Guerrero, E., Gil, D., & Macías Garcia, C. (2013). Dealing with urban noise: Vermilion flycatchers sing longer songs in noisier territories. *Behavioral Ecology and Sociobiology*, *67*(1), 145–152. https://doi.org/10.1007/s00265-012-1434-0

Ríos-Chelén, A. A., Salaberria, C., Barbosa, I., Macías Garcia, C., & Gil, D. (2012). The learning advantage: bird species that learn their song show a tighter adjustment of song to noisy environments than those that do not learn. *Journal of Evolutionary Biology*, *25*(11), 2171–2180.

Robertson, B., Kriska, G., Horvath, V., & Horvath, G. (2010). Glass buildings as bird feeders: urban birds exploit insects trapped by polarized light pollution. *Acta Zoologica Academiae Scientiarum Hungaricae*, *56*(3), 283–293.

Roell, A. (1978). Social Behaviour of the Jackdaw, Corvus Monedula, in Relation To Its Niche. *Behaviour*, *64*(1–2), 1–122.

Roughgarden, J., Running, S. W., & Matson, P. A. (1991). What does remote sensing do for ecology? *Ecology*, *72*(6), 1918–1922.

Russ, A., Rüger, A., & Klenke, R. (2015). Seize the night: European Blackbirds (Turdus merula) extend their foraging activity under artificial illumination. *Journal of Ornithology*, *156*, 123–131.

Ryer, A. (1997). *Light measurement handbook*. http://www.intl-light.com/handbook/.

Šálek, M., Grill, S., & Riegert, J. (2020). Nest-site selection of an avian urban exploiter, the Eurasian magpie Pica pica, across the urban-rural gradient. *Journal of Vertebrate Biology*, *70*(1), 20086-1.

Salvati, L. (2002). Nest site and breeding habitat characteristics in urban Jackdaws Corvus monedula in Rome (Italy). *Acta Ornithologica*, *37*(1), 15–19. https://doi.org/10.3161/068.037.0103

Sanderfoot, O. V, & Holloway, T. (2017). Air pollution impacts on avian species via inhalation exposure and associated outcomes. *Environmental Research Letters*, *12*(8), 083002.

Santiago-Alarcon, D., & Delgado-V, C. A. (2017). Warning! Urban threats for birds in Latin America. *Avian ecology in Latin American cityscapes*, 125-142. Springer, Cham. https://doi.org/10.1007/978-3-319-63475-3_7

Sayol, F., Sol, D., & Pigot, A. L. (2020). Brain Size and Life History Interact to Predict Urban Tolerance in Birds. *Frontiers in Ecology and Evolution*, *8*(March), 1–9. https://doi.org/10.3389/fevo.2020.00058

Schwartz, A. L. W., Williams, H. F., Chadwick, E., Thomas, R. J., & Perkins, S. E. (2018). Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology*, *4*(1), 1–7. https://doi.org/10.1093/jue/juy006

Seed, A., Emery, N., & Clayton, N. (2009). Intelligence in corvids and apes: A case of convergent evolution? *Ethology*, *115*(5), 401–420. https://doi.org/10.1111/j.1439-0310.2009.01644.x

Serjeantson, D. (2009). Birds. Cambridge Manuals in Archaeology. New York: Cambridge University Press.

Seto, K. C., Fleishman, E., Fay, J. P., & Betrus, C. J. (2004). Linking spatial patterns of bird and butterfly species richness with Landsat TM derived NDVI. *International Journal of Remote Sensing*, *25*(20), 4309–4324. https://doi.org/10.1080/0143116042000192358

Shannon, G., Crooks, K. R., Wittemyer, G., Fristrup, K. M., & Angeloni, L. M. (2016). Road noise causes earlier predator detection and flight response in a free-ranging mammal. *Behavioral Ecology*, *27*(5), 1370–1375. https://doi.org/10.1093/beheco/arw058

Shuai, L. Y., Morelli, F., Mikula, P., Benedetti, Y., Weston, M. A., Ncube, E., Tarakini, T., Díaz, M., Markó, G., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., & Cao, Y. Y. (2024). A meta-analysis of the relationship between flock size and flight initiation distance in birds. *Animal Behaviour*, *210*, 1–9. https://doi.org/10.1016/j.anbehav.2024.01.013

Slabbekoorn, H., & Ripmeester, E. A. P. (2008). Birdsong and anthropogenic noise: Implications and applications for conservation. *Molecular Ecology*, *17*(1), 72–83. https://doi.org/10.1111/j.1365-294X.2007.03487.x

Sol, D., Bartomeus, I., González-Lagos, C., & Pavoine, S. (2017). Urbanisation and the loss of phylogenetic diversity in birds. *Ecology Letters*, *20*(6), 721–729. https://doi.org/10.1111/ele.12769

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(15), 5460–5465. https://doi.org/10.1073/pnas.0408145102

Sol, D., González-Lagos, C., Moreira, D., Maspons, J., & Lapiedra, O. (2014). Urbanisation tolerance and the loss of avian diversity. *Ecology Letters*, *17*(8), 942–950. https://doi.org/10.1111/ele.12297

Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PloS one*, *6*(5), e19535.

Sol, D., Maspons, J., Gonzalez-Voyer, A., Morales-Castilla, I., Garamszegi, L. Z., & Møller, A. P. (2018). Risk-taking behavior, urbanization and the pace of life in birds. *Behavioral Ecology and Sociobiology*, *72*(3). https://doi.org/10.1007/s00265-018-2463-0

Sordello, R., Ratel, O., de Lachapelle, F. F., Leger, C., Dambry, A., & Vanpeene, S. (2020). Evidence of the impact of noise pollution on biodiversity: A systematic map. *Environmental Evidence*, *9*(1). https://doi.org/10.1186/s13750-020-00202-y

Stankowich, T., & Coss, R. G. (2007). Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behavioral Ecology*, *18*(2), 358–367.

Sun, J. W. C., & Narins, P. M. (2005). Anthropogenic sounds differentially affect amphibian call rate. *Biological Conservation*, *121*(3), 419–427.

Svensson, L., Mullarney, K., & Zetterström, D. (2010). Collins bird guide 2nd edition. *British Birds*, *103*, 248–252.

Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., & Reist, J. (2015). ecological niches and niche overlap R eports. *Ecology*, *96*(2), 318–324.

Szala, K., Dylewski, Ł., & Tobolka, M. (2020). Winter habitat selection of Corvids in an urban ecosystem. *Urban Ecosystems*, *23*(3), 483–493. https://doi.org/10.1007/s11252-020-00942-2

Tätte, K., Ibáñez-Álamo, J. D., Markó, G., Mänd, R., & Møller, A. P. (2019). Antipredator function of vigilance re-examined: vigilant birds delay escape. *Animal Behaviour*, *156*, 97–110. https://doi.org/10.1016/j.anbehav.2019.08.010

Taylor, L., & Hochuli, D. F. (2015). Creating better cities: how biodiversity and ecosystem functioning enhance urban residents' wellbeing. *Urban Ecosystems*, *18*(3), 747–762. https://doi.org/10.1007/s11252-014-0427-3

BirdLife International. (2015). European red list of birds. *Office for Official Publications of the European Communities, Luxembourg*.

Tidemann, S. C., & Gosler, A. (Eds.). (2012). *Ethno-Ornithology: birds, indigenous peoples, culture and society*. Earthscan.

Tietze, D. T. (2018). Introduction: studying birds in time and space. *Bird Species: How They Arise, Modify and Vanish*, 1–7.

Tobias, J. A., Ottenburghs, J., & Pigot, A. L. (2020). Avian Diversity: Speciation, Macroevolution, and Ecological Function. *Annual Review of Ecology, Evolution, and Systematics*, *51*, 533–560. https://doi.org/10.1146/annurev-ecolsys-110218-025023

Tryjanowski, P., Møller, A. P., Morelli, F., Biaduń, W., Brauze, T., Ciach, M., Czechowski, P., Czyz, S., Dulisz, B., Golawski, A., Hetmański, T., Indykiewicz, P., Mitrus, C., Myczko, L., Nowakowski, J. J., Polakowski, M., Takacs, V., Wysocki, D., & Zduniak, P. (2016). Urbanization affects neophilia and risk-taking at bird-feeders. *Scientific Reports*, *6*(June). https://doi.org/10.1038/srep28575

Tryjanowski, P., Sparks, T. H., Kuźniak, S., Czechowski, P., & Jerzak, L. (2013). Bird Migration Advances More Strongly in Urban Environments. *PLoS ONE*, *8*(5). https://doi.org/10.1371/journal.pone.0063482

Turner, W., Sterling, E. J., & Janetos, A. C. (2001). Introduction[to Special Section: Contributions of Remote Sensing to Biodiversity Conservation: A NASA Approach]. *Conservation Biology*, *15*(4), 832–834.

Tzortzakaki, O., Kati, V., Kassara, C., Tietze, D. T., & Giokas, S. (2018). Seasonal patterns of urban bird diversity in a Mediterranean coastal city: the positive role of open green spaces. *Urban Ecosystems*, *21*(1), 27–39. https://doi.org/10.1007/s11252-017-0695-9

UN DESA. (2019). World Urbanization Prospects: The 2018 Revision. *United Nations Department of Economic and Social Affairs: New York, NY, USA. Available online: https://www. un. org/en/development/desa/publications/2014-revision-worldurbanization-prospects. html.*

Van Doren, B. M., Willard, D. E., Hennen, M., Horton, K. G., Stuber, E. F., Sheldon, D., Sivakumar, A. H., Wang, J., Farnsworth, A., & Winger, B. M. (2021). Drivers of fatal bird collisions in an urban center. *Proceedings of the National Academy of Sciences*, *118*(24), e2101666118.

Vincze, E., Pipoly, I., Seress, G., Preiszner, B., Papp, S., Németh, B., Liker, A., & Bókony, V. (2019). Great tits take greater risk toward humans and sparrowhawks in urban habitats than in forests. *Ethology*, *125*(10), 686–701. https://doi.org/10.1111/eth.12922

Waite, R. K. (1984a). Sympatric Corvids : Effects of Social Behaviour, Aggression and Avoidance on Feeding. *Behavioral Ecology and Sociobiology*, *15*(1), 55–59.

Waite, R. K. (1984b). Winter Habitat Selection and Foraging Behaviour in Sympatric Corvids. *Scandinavian Journal of Ornitholog*, *15*(1), 55–62.

Wang, Y., Chen, S., Jiang, P., & Ding, P. (2008). Black-billed Magpies (Pica pica) adjust nest characteristics to adapt to urbanization in Hangzhou, China. *Canadian Journal of Zoology*, *86*(7), 676–684. https://doi.org/10.1139/Z08-045

Warren, P. S., Katti, M., Ermann, M., & Brazel, A. (2006). Urban bioacoustics: it's not just noise. *Animal behaviour*, *71*(3), 491-502.

Whittaker, R. H., Levin, S. A., & Rootj, R. B. (1973). Niche, Habitat, and Ecotope. *The University of Chicago Press*, *107*(955), 321–338. http://www.jstor.org/stable/2459534

Wolf, L. J., Zu Ermgassen, S., Balmford, A., White, M., & Weinstein, N. (2017). Is variety the spice of life? An experimental investigation into the effects of species richness on self-reported mental well-being. *PloS One*, *12*(1), e0170225.

Wright, D. H. (1983). Species-energy theory: an extension of species-area theory. *Oikos*, 496–506.

Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior* (16), 229–249.

Yoda, T. (2019). Managing Urban crow populations in Japan. *Human-Wildlife Interactions*, *13*(3), 439–446. https://doi.org/10.26077/7p56-2c75

Yorzinski, J. L., & Platt, M. L. (2014). Selective attention in peacocks during predator detection. *Animal Cognition*, *17*(3), 767–777. https://doi.org/10.1007/s10071-013-0708-x

Zhou, Y., Radford, A. N., & Magrath, R. D. (2019). Why does noise reduce response to alarm calls? Experimental assessment of masking, distraction and greater vigilance in wild birds. *Functional Ecology*, *33*(7), 1280–1289. https://doi.org/10.1111/1365-2435.13333

Zimaroyeva, A. A., Matsyura, A. V., & Jankowski, K. (2016). Spatial patterns of habitat distribution of Corvidae (the case of urban-rural gradient). *Biosystems Diversity*, *24*(2), 451–458. https://doi.org/10.15421/011661

Zmihorski, M., Halba, R., & Mazgajski, T. D. (2010). Long-term spatio-temporal dynamics of corvids wintering in urban parks of Warsaw, Poland. *Ornis Fennica*, *87*(2), 61–68.

Zollinger, S. A., Slater, P. J. B., Nemeth, E., & Brumm, H. (2017). Higher songs of city birds may not be an individual response to noise. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1860), 20170602.

CURRICULUM VITAE: Farah ABOU ZEID

Place of Birth: Haouch el Oumara, Lebanon; Place of Residence: Prague, Czech Republic
Phone : (420) 608 520 784 ; (961) 71 362 582 ; e-mail : farah.abouzeid21@gmail.com
ORCID: https://orcid.org/0000-0002-0686-143X

EDUCATION

2020 – *present*	**PhD in Applied and Landscape Ecology** (Czech University of Life Sciences Prague, Czechia) **Research** concerning the impacts of urbanization on bird communities.
2018 – 2019	**M2 in Environmental Expertise and Treatment** (University of the Littoral Opal Coats, France) Graduated with honors (mention bien).
2017 – 2019	**M.Sc. of Environmental Sciences** (University of Balamand, Lebanon) **Thesis Entitled:** "*Assessing Environmental and Economic Benefits of Urban Forests in the Governorate of Beirut*" ; (cGPA: 89.40/100.00 or 3.79/4.00)
Spring 2018	**ERASMUS+ Exchange semester** (University of Lleida, Spain) Courses from the "*Mediterranean Forestry and Natural Resource Management*" Program
2014 – 2017	**B.Sc. in Biology with a minor in Chemistry** (Lebanese American University, Lebanon) Graduated with Distinction (cGPA: 3.55/4.00)

CURRENT AFFILIATION

2020 – *present*	**Ph.D. Candidate** at the Czech University of Life Science in Prague. Community Ecology & Conservation Research Group; Ecology Department, Faculty of Environmental Sciences. Team leader and supervisor: Doc. Federico Morelli, Ph.D. Advisor: Dr. Yanina Benedetti, Ph.D.
2022-2023	**Funded Project:** the Internal Grant Agency (IGA) of the Faculty of Environmental Sciences, Czech University of Life Sciences (IGA 2022B0001): "*Investigating the impacts of urban noise pollution on the antipredator behavior of foraging corvids*" **Teaching experience:**
2021 – 2024	*Fundamentals of Ecology & General Ecology* (Department of Ecology)
2021 – 2022	*Workshop II* (Faculty of Environmental Sciences)

PREVIOUS WORK EXPERIENCE

Jul, Aug 2023	**Intern** (American University of Beirut, Nature Conservation Center; AUBNCC, Lebanon) **Research** concerning the impacts of cats on bird communities on the AUB campus.
2019 – 2020	**Middle School Science and Chemistry Teacher** (Second Official School of Jbeil, Lebanon)
2018 – 2019	**Project Assistant** (Lebanon Reforestation Initiative, Lebanon)
Sep-Dec 2017	**Student Assistant** (Institute of the Environment/University of Balamand, Lebanon)
Feb-Jun 2017	**Intern** (UNDP/Ministry of the Environment, Lebanon)
2014 – 2017	**Student Assistant** (Lebanese American University, Lebanon)

PUBLICATIONS

Abou-Zeid, F., Benedetti, Y., Siretckaia, A., & Morelli, F. (2024). Urban noise slows down the antipredator reaction of Eurasian Magpies. *Frontiers in Ecology and Evolution*, 12, 1345971. https://doi.org/10.3389/fevo.2024.1345971

Morelli, F., Benedetti, Y., Szkudlarek, M., **Abou Zeid, F.**, Delgado, J. D., & Kaczmarski, M. (2023). Potential hotspots of amphibian roadkill risk in Spain. *Journal of Environmental Managemen*t, 342, 118346. https://doi.org/10.1016/j.jenvman.2023.118346

Abou Zeid, F., Morelli, F., Ibáñez-Álamo, J. D., Díaz, M., Reif, J., Jokimäki, J., Suhonen, J., Kaisanlahti-Jokimäki, M.-L., Markó, G., Bussière, R., Mägi, M., Tryjanowski, P., Kominos, T., Galanaki, A., Bukas, N., Pruscini, F., Jerzak, L., Ciebiera, O., & Benedetti, Y. (2023). Spatial Overlap and Habitat Selection of Corvid Species in European Cities. *Animals*, 13(7), 1192. https://doi.org/10.3390/ani13071192

Benedetti, Y., Callaghan, C. T., Ulbrichová, I., Galanaki, A., Kominos, T., **Abou Zeid, F.**, Ibáñez-Álamo, J. D., Suhonen, J., Díaz, M., Markó, G., Bussière, R., Tryjanowski, P., Bukas, N., Mägi, M., Leveau, L., Pruscini, F., Jerzak, L., Ciebiera, O., Jokimäki, J., … Morelli, F. (2023). EVI and NDVI as proxies for multifaceted avian diversity in urban areas. *Ecological Applications*. https://doi.org/10.1002/eap.2808

Morelli, F., Mikula, P., Blumstein, D. T., Díaz, M., Markó, G., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Floigl, K., **Abou Zeid, F.**, Siretckaia, A., & Benedetti, Y. (2022). Flight initiation distance and refuge in urban birds. *Science of The Total Environment,* 842(June), 156939. https://doi.org/10.1016/j.scitotenv.2022.156939

Abou Zeid, F. (2019). Assessing environmental benefits of urban forests and associated economic values of carbon dioxide reduction in the Mohafazat of Beirut [Masters]. University of Balamand.

SCIENTIFIC CONFERENCE CONTRIBUTION

2022	**Kostelecké inspirování**, poster presentation: *"Investigating the Antipredator Behavior of Jackdaws and Magpies in Prague's Urban Parks"*
2021	**6th Global Biodiversity Conservation Conference**, poster presentation: *"Distribution of Corvids Along a Gradient of Urbanization Within European Cities"*
2020	**Kostelecké inspirování**, poster presentation: *"Assessing environmental benefits of urban forests and resulting economic values of carbon dioxide removal. A case study from Lebanon"*

SCIENTIFIC REFEREE

Sept, 2023	*EcoScience*
May, 2024	*Frontiers in Ecology and Evolution*

LANGUAGE SKILLS

English	Fluent
French	Fluent
Arabic	Mother tongue

COMPUTER SKILLS

Microsoft office	Excel, Word, PowerPoint ●●●●●
Mapping	ArcGIS, QGIS ●●●●○
Data analysis	RStudio ●●●●○

OTHER SKILLS

Scientific writing, literature reviews, grant proposal writing, data analysis, field data collection of the Flight Initiation Distance, and mapping.

ANNEX SECTION

Annex I. Spatial overlap and habitat selection of corvid species in European cities.

Farah Abou Zeid* , Federico Morelli, Juan Diego Ibáñez-Álamo, Mario Díaz, Jiří Reif, Jukka Jokimäki, Jukka Suhonen, Marja-Liisa Kaisanlahti-Jokimäki, Gábor Markó, Raphaël Bussière, Marko Mägi, Piotr Tryjanowski, Theodoros Kominos, Antonia Galanaki, Nikos Bukas, Fabio Pruscini, Leszek Jerzak, Olaf Ciebiera, and Yanina Benedetti, 2023.

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Article

Spatial Overlap and Habitat Selection of Corvid Species in European Cities

Farah Abou Zeid [1,*], Federico Morelli [1,2], Juan Diego Ibáñez-Álamo [3], Mario Díaz [4], Jiří Reif [5,6], Jukka Jokimäki [7], Jukka Suhonen [8], Marja-Liisa Kaisanlahti-Jokimäki [7], Gábor Markó [9], Raphaël Bussière [10], Marko Mägi [11], Piotr Tryjanowski [12], Theodoros Kominos [13], Antonia Galanaki [13], Nikos Bukas [14], Fabio Pruscini [15], Leszek Jerzak [2], Olaf Ciebiera [2] and Yanina Benedetti [1]

[1] Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 00 Prague, Czech Republic; fmorellius@gmail.com (F.M.); ybenedetti73@gmail.com (Y.B.)

[2] Institute of Biological Sciences, University of Zielona Góra, Prof. Z. Szafrana St. 1, 65-516 Zielona Góra, Poland; l.jerzak@wnb.uz.zgora.pl (L.J.); o.ciebiera@wnb.uz.zgora.pl (O.C.)

[3] Department of Zoology, Faculty of Sciences, University of Granada, 18071 Granada, Spain; jia@ugr.es

[4] Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (BGC-MNCN-CSIC), 28006 Madrid, Spain; mario.diaz@mncn.csic.es

[5] Institute for Environmental Studies, Faculty of Science, Charles University, Prague, Benatska 2, 128 01 Praha, Czech Republic; jirireif@natur.cuni.cz

[6] Department of Zoology, Faculty of Science, Palacky University in Olomouc, 17. Listopadu 50, 771 46 Olomouc, Czech Republic

[7] Nature Inventory and EIA-Services, Arctic Centre, University of Lapland, P.O. Box 122, 96101 Rovaniemi, Finland; jukka.jokimaki@ulapland.fi (J.J.); marja-liisa.kaisanlahti@ulapland.fi (M.-L.K.-J.)

[8] Department of Biology, University of Turku, 20014 Turku, Finland; juksuh@utu.fi

[9] Department of Plant Pathology, Institute of Plant Protection, Hungarian University of Agriculture and Life Sciences, Ménesi út 44, 1118 Budapest, Hungary; magvacska@gmail.com

[10] 4 Route de la Loge, 86800 Liniers, France; raphael.bussiere87@gmail.com

[11] Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, 50409 Tartu, Estonia; markomagi78@gmail.com

[12] Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625 Poznań, Poland; piotr.tryjanowski@gmail.com

[13] Department of Zoology, School of Biology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece; tkominos@hotmail.com (T.K.); antgalanaki@gmail.com (A.G.)

[14] Plegadis, Riga Feraiou 6A, 45444 Ioannina, Greece; bionickbukas@hotmail.com

[15] S. C. della Pantiera 23, 61029 Pantiera, Italy; fabiopruscini@libero.it

[*] Correspondence: farah.abouzeid21@gmail.com

Simple Summary: Many corvid species have adapted to live in urban regions. Studying their habitat needs and the similarities among them would allow us to predict species' responses to global changes. Such studies have not been widely done on generalist species capable of surviving in different environments. Here, we studied the habitat needs and spatial overlap of five corvid species in sixteen European cities. We found significant overlap in the habitats of the corvids, although some had different tendencies. Three species (the Carrion/Hooded Crow, Rook, and Eurasian Magpie) selected open habitats (grass or bare soil). The Eurasian Jay chose more forested areas, and the Western Jackdaw avoided areas with bare soil cover. The species that had similar habitat tendencies also had similar spatial distributions. Our results show that even corvids with different tendencies overlapped highly in their habitats, which means they can tolerate different environmental conditions in urban areas.

Abstract: Understanding habitat and spatial overlap in sympatric species of urban areas would aid in predicting species and community modifications in response to global change. Habitat overlap has been widely investigated for specialist species but neglected for generalists living in urban settings. Many corvid species are generalists and are adapted to urban areas. This work aimed to determine the urban habitat requirements and spatial overlap of five corvid species in sixteen European cities during the breeding season. All five studied corvid species had high overlap in their habitat selection while still having particular tendencies. We found three species, the Carrion/Hooded Crow, Rook, and Eurasian Magpie, selected open habitats. The Western Jackdaw avoided areas with bare soil cover,

and the Eurasian Jay chose more forested areas. The species with similar habitat selection also had congruent spatial distributions. Our results indicate that although the corvids had some tendencies regarding habitat selection, as generalists, they still tolerated a wide range of urban habitats, which resulted in high overlap in their habitat niches and spatial distributions.

1. Introduction

Although urban areas occupy less than 3% of the total land cover, their impacts reach areas several times larger [1,2]. Additionally, as the urban population is expected to rise to 84% in Europe by 2050, urban land cover is expected to increase even at a greater speed than the population [1,3]. Urban areas are characterized by increased levels of anthropogenic disturbance, noise, light and air pollution, meso-predators (i.e., cats and dogs), and altered environments [4–6]. As a result, new environments in which only a few species can survive are created due to urbanization constraints [7], leading to urban communities that are biotically homogenized [8]. Biotic homogenization is characterized by replacing many native, specialist, and endemic species with a few widespread generalists, leading to increasingly similar communities and a reduction in global biodiversity [7,9].

Many corvid species are generalists that adjust to urbanization and anthropogenically modified areas [10–13]. Most research has reported a positive impact of urbanization on corvids and an increase in their abundance along urbanization gradients [14]. Corvids are intelligent birds with a large brain-to-body mass ratio whose intelligence is comparable to some primates [15]. Their advanced cognition is one of the reasons they are able to thrive amidst urbanization by increasing their innovation to better adapt to new circumstances [15,16]. Corvids may exploit new nesting sites created within artificial structures, such as buildings, poles, tram tracks, and power lines [14,17,18]. Moreover, their omnivore diet allows them to consume different urban foods [15]. Furthermore, decreased predation and persecution pressure in cities are essential factors promoting corvids' living in urban settings [14]. Due to the low persecution level and anthropogenic food sources in cities, many corvid species have habituated to humans, a factor that further fosters their urbanization [19].

In urban areas, corvids have several impacts on the environment that affect the local people both positively and negatively and, therefore, play a role in the ecosystem services and disservices [20]. Corvids provide several ecosystem services in urban areas as they are seed dispersers of oak and pine trees, could serve as biosensors for the early detection of hazardous contaminating agents (e.g., West Nile Virus), and are considered model organisms of urban ecology studies [14,21,22]. These birds also cause ecosystem disservices as they forage in trash cans, spread waste and possibly diseases, and are known for inducing agricultural and infrastructural damage and causing noise [12,14,23,24]. Corvids are nest predators, and their increased presence in urban areas may limit the nesting capacities of other species, reducing the region's biodiversity [25–29]. Therefore, detailed knowledge of species' habitat requirements could contribute to more efficient management of corvids populations in cities when needed [29].

Several studies have looked into the urban habitat selection of corvids [13,30–32] and in Europe specifically [18,19,33–35]. Most of these studies were only conducted in one city or focused on a single corvid species [19]. Thus, there is still a need for large-scale, meta-replicating studies concerning the urban habitat selection of corvids across species and sites to obtain general findings [36].

Hutchinson defined the realized niche as the environmental conditions where a species can survive, reproduce, and grow despite predators and competitors [37]. The ecological niche governs the distribution of the species and can be considered an n-dimensional hypervolume, where n is the number of ecological factors considered [37,38]. Sympatric

species are simultaneously present in the same area [39]. Understanding habitat niche and spatial overlap in guilds of sympatric species in urban areas could aid in predicting both species and community changes in response to global change.

Niche overlap among sympatric birds has been studied extensively in specialist species but neglected in generalist species with broader niches [40]. Some studies have addressed sympatry among corvids outside urban areas [41–44]. However, studies assessing habitat overlap in corvids in urban areas have been lacking [40].

This study aims to characterize the habitat selection and the degree of spatial overlap among five corvid species inhabiting different European cities. Specifically, we will (1) investigate the presence and distribution of each corvid species in 16 European cities, (2) assess the level of spatial overlap among the five corvid species, (3) understand the level of overlap of their habitat selection, and (4) determine the urban features selected by each species. We hypothesize that due to the differences in body sizes and nest sites, the habitat selection of corvids will differ and that species with similar habitat requirements will have similar spatial distributions. We predict that larger species (the Carrion/Hooded Crow; *Corvus corone/cornix*, Rook; *Corvus frugilegus*, and Eurasian Magpie; *Pica pica*) will pick out more open sites. We believe smaller species (the Eurasian Jay; *Garrulus glandarius*) will choose more vegetated, closed sites. Hole-nesting corvids (the Western Jackdaw; *Corvus monedula*) will select built-up areas. We used the point count method to study the presence and abundance of corvids in the 16 European cities depending on the characteristics of the sites. We then examined the mismatch between their spatial distributions and the level of their habitat niche overlap and modeled the habitat selection of each corvid species.

2. Materials and Methods

2.1. Study Area

In 2018, sixteen European cities (Figure 1) were surveyed during the breeding season. Data on corvid species' presence and abundance were collected through standardized single-visit point counts [45,46]. We used the point count method to collect data regarding breeding corvids, as we were not interested in roosting corvid flocks that may only overnight in the cities [14]. In each city, around one hundred point counts, with a circle of a 50 m radius, were used for data collection (more information regarding the exact number of point counts in each city, along with the population and population density, is presented in Table S1). All point counts were at least 500 m from the city borders to avoid sampling transitional suburban regions. The distance between any two point counts was more than 100 m to avoid double-counting the same corvid individuals. The point counts were uniformly distributed along a gradient of urbanization (i.e., at the inner core area of the city, the surrounding area of the inner core area, and the less urbanized residential areas) in each city to sample different corvid species with different urban habitat preferences equally.

2.2. Field Data Collection

Sampling was started just after sunrise in cities other than Rovaniemi, where the sun does not set during the mid-summer. In Rovaniemi, surveys began at 02.00 a.m. The surveys were ended before the heavy morning traffic started in each study area (i.e., around 07.00 a.m.). Sampling was conducted in favorable weather conditions (no rain or strong wind) and for 5 min per sampling site following standard bird survey methodology used in previous studies on urban birds [45,47,48]. The data were collected during the peak breeding season depending on the city (e.g., May in Southern Spain vs. June in Finland) to maintain a similar detectability of birds between the different cities [49]. The location of each point count was recorded using a GPS to find other characteristics regarding the site (described in the following section). All corvid species and individuals heard or seen within the 50 m radius of the point counts were recorded. Overflying individuals that did not land within the study circle were excluded.

Figure 1. Map of the sixteen European cities surveyed.

2.3. Variables Studied in Terms of Corvid Habitat Selection

After the bird surveys, information regarding the vegetation cover and land use composition was collected to study the corvids' habitat characteristics. Local-scale variables were shown to have more influence on the species distribution than regional ones [50]. For that reason, we collected patch-level variables (the percentages of built (impervious), tree (single trees, lines of trees, and tree patches), bush, grass, and bare soil covers; refs. [51–54], a matrix level variable (the average number of building floors); ref. [55], and disturbance variables (number of cats, dogs, and pedestrians) [6,56]; which were determined visually by the observers within the 50 m radius point count and during the five minutes bird survey period. Other disturbance variables were calculated for each point count. We included light and noise pollution variables while assessing the habitat characteristics of the corvids as these variables have been shown to influence birds' habitat selection [47,57–59].

Each point count was georeferenced. The coordinates of each study circle were used to extract light pollution information from the VIIRS satellite (from the website: https://www.lightpollutionmap.info). The values, precalculated on the website, were extracted for 2018 (here, average yearly values were used) and correspond to the Radiance 10^{-9}W/cm^2 * sr (W = Watts and sr = steradian) [60].

Noise pollution models were performed using the open noise tool (https://plugins.qgis.org/plugins/opeNoise) for QGIS. This tool permits measuring in 2D space (e.g., around point counts) the mean noise from point or road sources received at fixed points and buildings. Noise sources were based on Urban Atlas land use categories, and buildings from Open Street Map (OSM) were used as an advanced input for diffraction and noise reduction. Noise spreading in a 250 m range of each source (point) was calculated. The

results consisted of model-based mean noise levels in dB in a radius of 50 m around the point counts [60].

2.4. Classification of the Carrion Crow and the Hooded Crow

In 2003, the Hooded Crow was recognized as a separate species from the Carrion Crow due to the positive assortative mating of the two taxa and the reduced fitness of their hybrids [61]. Thus, information regarding each species separately is still lacking and they are often described as both species merged as one [62–65]. Debate remains regarding the taxonomic classification of the two taxa, where it may seem that they are still in the early stages of speciation [66,67]. From a genetic perspective, their only main difference is possibly their plumage coloration [67,68]. Finally, since both taxa use similar environments in geographically separate areas, estimating their habitat selection and overlap separately may lead to misleading results. For these reasons, we merged the observations of the Carrion Crow and the Hooded Crow and considered them as one species.

2.5. Statistical Analyses

To test spatial overlap among the corvid species, we used the spatial mismatch analysis through a Mantel test [69] with the package "ade4" in R [70]. The Mantel test quantifies correlations between two distance matrices using the coefficient RM, which varies between −1 and 1 and behaves similarly to a correlation coefficient. Here, the distance matrices were developed among point counts on the abundance of each corvid species. Monte Carlo permutations, with 999 randomizations, were employed to test for significance.

The nicheROVER package of R [71] was used to estimate the probabilistic niche regions of each species. For each species, point counts where the species was present were used, and then a directional probabilistic niche overlap of each pair of corvid species was deduced for their habitat selection [72]. The niche region is defined as "a 95% probability region in multivariate space", estimated using 1000 Monte Carlo draws and alpha = 0.95. Niche overlap is then calculated as the posterior probability that an individual from the first species was found within the niche region of the other species and vice versa [72]. The advantages of this approach are that it gives a directional niche overlap metric (overlap of species A into B is different from that of species B into A) and that it accounts for uncertainty using a Bayesian framework. Furthermore, this method is not sensitive to sample size [72]. The latter is particularly useful for calculating overlap among species with different distributions, such as in the case of some pairs of species in our study (i.e., the Western Jackdaw and all other species studied) [73].

Generalized Linear Mixed Models (GLMMs) using a binomial distribution were fitted to assess the characteristics of the habitats used by each corvid species by relating the presence/absence of a corvid species in a point count to the respective predictors. The predictors tested were: the number of cats, dogs, building floors, and pedestrians; the percentage of grass, tree, bare soil, and bush cover; and the amount of light and noise pollution within 50 m around the point counts. The percentage of the built area was dropped for being highly correlated to the percentage of grass cover (VIF > 6). The city (*n* = 14; Rovaniemi and Zielona Góra were excluded from the models for having missing values in the light and noise pollution predictors, making the sample size for the models *n* = 1288) was incorporated as the random factor to account for variation among the different cities. R package "lme4" was used to fit the models [74]. "Dredging" was used from the R package "MuMIn" [75] to form and rank all possible model combinations using the predictors. Second-order Akaike Information Criterion (AICc) was used to select the best models. Model averaging was performed on top models with ΔAICc < 4 (detailed in Supplementary Table S2) to address problems related to selection uncertainty [76] using the MuMIn package.

All analyses were performed using R software version 4.0.3 [77].

3. Results

After removing only two observations of the Common Raven (*Corvus corax*), 2324 corvid individuals belonging to five species (the Carrion/Hooded Crow, Rook, Western Jackdaw, Eurasian Jay, and Eurasian Magpie) were recorded in 1462 point counts surveyed in sixteen European cities (Figures 1 and S1).

The Eurasian Magpie was the species most spread in the study area. It was observed in all cities (Figures S2 and S3). The Western Jackdaw was the most abundant corvid and was detected in most cities except Athens, Budapest, and Madrid. The Carrion/Hooded Crow was present in most surveyed cities except Granada, Madrid, and Toledo. The Eurasian Jay was observed in eight cities (Athens, Budapest, Groningen, Ioannina, Poitiers, Poznan, Prague, and Zielona Góra). The Rook was the least detected and least abundant corvid and was only present in five of the sixteen studied cities (Groningen, Poitiers, Poznan, Prague, and Tartu).

3.1. Spatial Overlap

The distribution of the Carrion/Hooded Crow was congruent with that of the Rook, Eurasian Jay, and Eurasian Magpie (Table 1). The distribution of the Eurasian Magpie was also slightly congruent with those of the Rook and Eurasian Jay. The spatial distribution of the Western Jackdaw did not match that of any other corvid. The spatial distributions of the Rook and the Eurasian Jay were not congruent. Congruent distributions mean that the species pair had a similar variation in abundance across the point counts.

Table 1. Spatial overlap test. Results of Mantel tests between the spatial distributions of each pair of corvid species, with 999 Monte Carlo permutations. The table shows the statistic RM of the test and the simulated *p*-values. Values with a *p*-value < 0.05 are in bold.

Variables Correlated	RM	*p*-Value
Carrion/Hooded Crow × Rook	**0.100**	**<0.01**
Carrion/Hooded Crow × Western Jackdaw	−0.010	>0.05
Carrion/Hooded Crow × Eurasian Jay	**0.110**	**<0.01**
Carrion/Hooded Crow × Eurasian Magpie	**0.150**	**<0.001**
Rook × Western Jackdaw	0.035	>0.05
Rook × Eurasian Jay	−0.016	>0.05
Rook × Eurasian Magpie	**0.084**	**<0.01**
Western Jackdaw × Eurasian Jay	−0.002	>0.05
Western Jackdaw × Eurasian Magpie	0.010	>0.05
Eurasian Jay × Eurasian Magpie	**0.080**	**<0.01**

3.2. Habitat Selection

The probabilistic niche overlap between two species is not necessarily identical. This approach gives a directional niche overlap metric (overlap of species A into B is different from that of species B into A) [72]. The overlap of habitat use was high between each pair of corvids, with the probability of overlap of all pairs being higher than 80%, except for the Rook (Figure 2). The probability that any corvid individual overlaps the habitat niche region of the Rook was below 40%. On the other hand, the probability that a Rook individual would overlap the habitat niche region of any other corvid was higher than 85%.

Specifically, the percent cover of bare soil and grass were the two most important variables to characterize the habitat use of all corvid species (Table 2). The Carrion/Hooded Crow presence was positively correlated to bare soil and also to grass cover as the Rook. The presence of the Western Jackdaw was negatively correlated to the cover of bare soil. The Eurasian Jay's presence was positively correlated to the percentage of tree cover. The Eurasian Magpie's presence positively correlated to bare soil, grass cover, and noise level. However, it was negatively correlated to the number of pedestrians present. No corvid species' presence was significantly correlated to the number of cats, dogs, building floors or the amount of light within the 50 m radius.
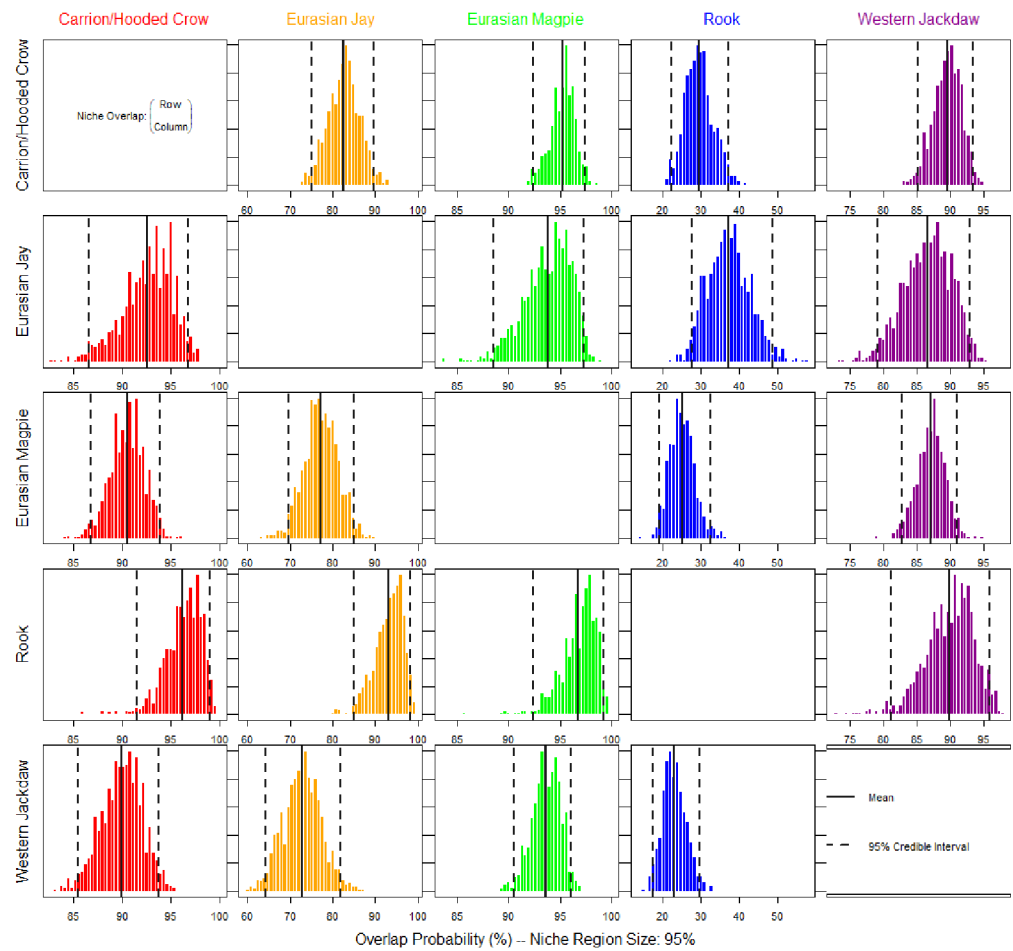
Figure 2. Posterior distribution of the probabilistic niche overlap metric for corvid species in urban areas, considering the land use composition. The posterior mean and 95% credible interval are indicated with black lines and give the probability that species displayed in rows overlap onto those displayed in columns.

Table 2. Habitat selection models. Results of the model averaged coefficients of the GLMMs relating corvid species' presence/absence to urban habitat characteristics. The predictors include the noise and light pollution, the percentage of bare soil, grass, tree, and bush cover, and the number of pedestrians, cats, and dogs present in the 50 m radius around the point counts. The city ($n = 14$) was used as a random factor. A separate model was run for each corvid species. For each species, dredging was used to generate all models based on the various combinations of predictors. Models with $\Delta AICc < 4$ (top models are detailed in Supplementary Table S2.) were averaged to give the results in the table. Estimates with a *p*-value < 0.05 are in bold.

Variable	Estimate	SE	z-Value	*p*-Value
		Carrion/Hooded Crow		
Intercept	−3.050	0.737	4.141	$p < 0.001$
Bare soil	**0.022**	0.007	2.977	**0.003**
Building floors	0.068	0.048	1.421	0.155
Bush	0.002	0.008	0.192	0.848
Cats	−0.019	0.083	0.224	0.823
Dogs	0.118	0.074	1.595	0.111
Grass	**0.016**	0.005	3.200	**0.001**
Light	−0.000	0.004	0.058	0.954
Noise	−0.007	0.011	0.587	0.557
Pedestrians	−0.008	0.004	1.756	0.079
Tree	−0.000	0.006	0.069	0.945

Table 2. *Cont.*

Variable	Estimate	SE	z-Value	p-Value
		Rook		
Intercept	−5.551	1.952	2.843	0.004
Bare soil	0.019	0.017	1.115	0.265
Building floors	−0.173	0.139	1.246	0.213
Bush	−0.044	0.026	1.706	0.088
Cats	−0.012	0.292	0.041	0.968
Dogs	−0.390	0.291	1.343	0.179
Grass	**0.034**	0.011	2.947	**0.003**
Light	−0.016	0.016	0.990	0.322
Noise	0.004	0.031	0.139	0.890
Pedestrians	−0.010	0.019	0.512	0.609
Tree	−0.034	0.018	1.923	0.055
		Western Jackdaw		
Intercept	−1.605	0.7629	2.104	0.035
Bare soil	**−0.016**	0.0070	2.350	**0.019**
Building floors	0.053	0.038	1.374	0.170
Bush	−0.008	0.008	0.922	0.357
Cats	0.043	0.086	0.498	0.619
Dogs	−0.140	0.084	1.665	0.096
Grass	−0.009	0.005	1.736	0.083
Light	0.004	0.003	1.304	0.192
Noise	−0.009	0.011	0.800	0.424
Pedestrians	0.000	0.002	0.198	0.843
Tree	−0.010	0.006	1.557	0.120
		Eurasian Jay		
Intercept	−4.795	1.551	3.092	0.002
Bare soil	0.005	0.012	0.419	0.675
Building floors	−0.238	0.135	1.766	0.077
Bush	0.017	0.013	1.331	0.183
Cats	0.131	0.105	1.250	0.211
Dogs	0.089	0.112	0.796	0.426
Grass	0.010	0.010	1.041	0.298
Light	−0.012	0.009	1.322	0.186
Noise	0.026	0.021	1.237	0.216
Pedestrians	−0.027	0.015	1.767	0.077
Tree	**0.019**	0.009	2.186	**0.029**
		Eurasian Magpie		
Intercept	−2.914	0.695	4.191	<0.001
Bare soil	**0.015**	0.006	2.776	**0.006**
Building floors	0.021	0.030	0.709	0.478
Bush	0.002	0.007	0.245	0.806
Cats	0.004	0.075	0.053	0.957
Dogs	−0.025	0.062	0.401	0.689
Grass	**0.027**	0.004	6.644	**<0.001**
Light	−0.003	0.003	1.151	0.250
Noise	**0.021**	0.009	2.359	**0.018**
Pedestrians	**−0.012**	0.004	3.385	**<0.001**
Tree	−0.003	0.005	0.645	0.519

4. Discussion

4.1. Corvids' Abundance and Distribution in Urban Areas

The Eurasian Magpie was the most widespread species and present in all sixteen surveyed European cities (Figures S1 and S2). The species started colonizing Eurasian cities during the second half of the twentieth century [34,78,79]. Magpies are omnivorous and sedentary, traits facilitating a bird's presence in urban environments [80]. Eurasian Magpies could modify their behavior to adapt to urban areas and have already undergone

synurbanization in several cities [31,33–35,81]. For example, the bird tends to nest higher in trees as urbanization levels increase [32,33,35]. In urban areas, the Eurasian Magpie increases the share of the nests it builds in conifers, especially in early spring when deciduous trees are leafless and exposed [33,34]. These adaptations probably allow Eurasian Magpie individuals to avoid human disturbance and nest predation from pets and Carrion Crows [32–34]. The decrease in persecution is another apparent reason for the urbanization of the Eurasian Magpie [34].

The *Corvus* genus is an especially successful genus within the Corvidae family. Their successful global expansion (as they occupy all continents but Antarctica) is due to their capacity to disperse over long distances and their high ability to survive in suboptimal and adapt to new environments [10]. The Western Jackdaw was the most abundant species (Figures S1 and S2). As a cavity nester, the species has adapted to use buildings and other anthropogenic cavities for nesting in urban areas [11,17,82,83]. In Slovenia, a study found that more than 80% of Western Jackdaw pairs nest in buildings [17]. The Western Jackdaw is also an omnivore and somewhat sedentary, so adaptation to urbanization is no surprise [84].

The Carrion/Hooded Crow was also abundant and widespread (Figures S1 and S2). The Carrion/Hooded Crow has also been frequently associated with urbanization, anthropogenically modified areas, and anthropogenic food resources [12]. The Carrion/Hooded Crow has benefitted from the decreased persecution [85]. The Carrion/Hooded Crow, Western Jackdaw, and Eurasian Magpie were the three most common corvids observed in a study conducted during the winter season in urban areas of Finland [19].

Our study, conducted during the breeding season, showed that the Eurasian Jay and Rook were the least spread and abundant species (Figures S1 and S2). The densities of the Rook are declining in Europe, and the bird has been listed as vulnerable on the European Red List of Birds [86]. Additionally, the Rook and Eurasian Jay have been previously demonstrated to utilize cities more often during the winter, perhaps to use warmer temperatures and ample food supplies. For the breeding season, both species probably move to nearby villages to nest and feed in more natural areas, which explains the low number of their records in our sample [11,87–89]. In addition, the Eurasian Jay has not yet become urbanized in some regions, such as Finland [19].

4.2. Corvids' Urban Habitat Selection

Understanding the habitat requirements of corvids in urban areas could aid efforts to control their populations and reduce their negative impacts [14,29]. Our large-scale study investigated the urban habitat of five corvid species in sixteen European cities during the breeding season. Although some species showed different habitat selections, the majority (the Carrion/Hooded Crow, Rook, and Eurasian Magpie) were positively linked to open spaces (grass and bare soil cover; Table 2). This selection may be related to their feeding habits because various studies have shown that the abundance and habitat selection of corvids in cities were influenced by food availability [12,24,40]. Although they use anthropogenic food sources such as waste disposal sites, they also rely on insects, snails, and earthworms, especially during the breeding season, to provide their juveniles with nutritious food [12,15,84,90]. Therefore, their presence increases near open grass and bare soil fields where they could be foraging for these valuable resources. Another advantage of open habitats is the early detection of predators since few structures obscure their vision [91]. As corvids are relatively heavy birds, they require longer to flee from approaching predators, so early detection of predators may be valuable [92]. Other studies also found a positive correlation between open spaces and corvids within and outside of urban areas, especially grasslands [18,89,93–95]. The Western Jackdaw was the only corvid negatively impacted by bare soil cover (Table 2). Here, the percentage of the built surface was dropped from the models as it was highly and negatively correlated to the portion of grass and, to a lesser extent, bare soil. More extensive coverage of bare soil would translate to a smaller cover of built-up areas. Unlike the other corvids in this study, the Western

Jackdaw, as a cavity nester, is known to nest in buildings [17,32,82,83], which could explain its negative correlation to bare soil cover, resulting from reduced built-up areas and, thus, nesting sites. Outside of urban areas, the Western Jackdaws are found in farmlands, rocky habitats, or a mix of both, where they can have nesting and feeding sites [83]. Other studies found a positive correlation between the Western Jackdaw abundance and city centers or densely built-up areas [52,83,96]. Within urban areas, Salvati (2002), found that the optimal habitat of the Western Jackdaw consists of a mixture of old buildings, ruderal zones, open areas, and small green areas [83]. From our results, it seems that the built cover is the most important of these factors and that Western Jackdaws may choose regions with more extensive built cover and smaller open land covers for breeding. There might even be a mismatch between the nest sites of urban Western Jackdaw individuals and their optimal foraging habitats [84], which suggests regular movements of the species between nesting sites (in cities) and foraging sites (their surroundings), and hence an effect of city size on the Western Jackdaw's presence. The Eurasian Jay was not linked to the cover of the open areas (Table 2). It was the only corvid in this study positively influenced by tree cover. It is not surprising as the Eurasian Jay has been considered a typical forest dweller associated with forest cover [11,97], is still in the process of colonizing urban areas [93,98], and is more correlated to the least urbanized sectors of a city [99]. Moreover, the Eurasian Jay may actively increase the tree cover of a city because this species is considered an efficient disperser of acorn through a mutualistic relationship with oak species [97,100,101]. Another study showed a positive correlation between the Eurasian Jay and woody vegetation in an urban area, matching our findings [93]. None of the corvids studied seemed to be impacted by the amount of light (Table 2). These results differ from those of another study that found that the densities of the Rook and Eurasian Magpie increased with light pollution levels and decreased with the noise level in southern Poland [58]. The different spatial scales and the fact that the former study was conducted during the winter season may explain these differences. In contrast, our results only showed a positive relationship between noise pollution and the presence of the Eurasian Magpie and no impact on other corvids (Table 2). Some species may benefit from higher noise levels due to the disruption of predator–prey interactions, which may be the case of the Eurasian Magpie [59]. The Eurasian Magpie was also the most widespread corvid in our study. Both results suggest that the Eurasian Magpie is a flexible corvid and the most tolerant to urban noise pollution in the European cities studied. Still, all corvid species studied are well adapted to urban noise and not heavily impacted by it. Similarly, another study found that the Eurasian Magpie and Western Jackdaw were linked to areas with increased noise levels [52]. The Eurasian Magpie was also the only corvid impacted by the density of pedestrians. The amounts of cats and dogs affected none of the corvids studied. Although these mesopredators may be more abundant in urban areas, predation rates are lower as they may be relying on anthropogenically abundant food, shifting their diets away from vertebrate prey, something corvids may have caught up with [6,102].

4.3. Corvids' Spatial and Habitat Overlap

The habitat selection of the corvids could explain their spatial distributions and level of habitat overlap. The distribution of the Western Jackdaw was not congruent with any other corvid (Table 1). We assume this is due to the Western Jackdaw's preference for built-up and heavily dense areas [96], unlike the other corvids. The Carrion/Hooded Crow, Rook, and Eurasian Magpie were linked to open spaces, and their distributions were congruent (Tables 1 and 2). The Eurasian Jay was the only one related to the tree cover, unlike other corvids, its distributions matched those of the Eurasian Magpie and Carrion/Hooded Crow. This could be due to their occurrence in large urban open spaces, such as parks, where large open spaces and tree covers coincide, benefiting both species similarly. The distribution of the Eurasian Jay was not congruent with that of the Rook. We assume this is caused by the low presence of both species in this study.

We found a high overlap in this study's habitat niches of all five corvid species (Figure 2). High habitat overlap of four corvids (the Carrion/Hooded Crow, Rook, Western Jackdaw, and Eurasian Magpie) was also found in winter in agricultural areas in Britain [95]. Here, except for the Rook, the probability that any corvid overlapped another corvid's habitat niche region was very high [95]. The probability that another corvid overlapped the niche of the Rook was low but high the other way around. This indicates that the Rook has a smaller niche region, almost completely embedded in the different corvids' niches. We expect Rooks to broaden their urban habitat niches during the winter when they are more likely to occupy this environment [96]. The Eurasian Magpie, followed by the Carrion/Hooded Crow, had the largest niches that highly overlap and almost embed to a large extent within them the majority of the habitat niches of other species. The Eurasian Magpie also had the largest overlap in foraging behavior with other corvids in another study [41]. As for the Western Jackdaw and Eurasian Jay, although they highly overlapped, they had the least habitat niche overlap between them, perhaps because the Eurasian Jay selected more natural areas [98], and was correlated to tree cover, while the Western Jackdaw may select built-up areas [83,96].

While some corvids seemed to select similar habitats in urban areas (the Eurasian Magpie, Carrion/Hooded Crow, and Rook), others had different tendencies (the Western Jackdaw and Eurasian Jay), they still overlapped quite extensively in their habitat niches (Table 1, Figure 2). In addition, although their niches highly overlapped, the corvids distributions were congruent only with those with similar tendencies. We can infer that corvids can tolerate a wide array of ecological conditions in urban regions but still have some preferences [14]. They are intelligent birds with an omnivore diet which aids them in broadening their ecological niches by adapting to novel environments and using different foods [12,15,16]. Thus, behavioral adaptations might play an essential role in adapting species to novel environments, especially in unstable or disturbed ones [10]. The high habitat overlap paired with increased congruent distributions between species of similar habitat selection could also be explained by the fact that birds have only started to colonize urban areas recently. Their urban populations may not have yet reached the carrying capacity and resource limitations of the environment, and thus, the pressure upon those closely related species that need to acquire interspecific differentiation may be still too weak, enabling their coexistence even in the presence of broad niche overlap [103,104]. In addition, high disturbance regimes, such as urban areas, tend to allow the coexistence of generalists with overlapping niches [105]. Alternatively, since their habitats overlap largely, we think other factors, unaccounted for in this study, may determine separation in their resource use. For example, while four corvids highly overlapped in their foraging habitats, their overlap in their prey type intakes was low [41]. Moreover, vast morphological differences in the skulls of corvids were noted, which were attributed to their differences in foraging modes [106]. In an urban study, two sympatric crow species were found to differ in feeding behaviors and feeding habitat, while their food preferences overlapped extensively [40]. Thus, interspecific relationships (i.e., territoriality and dominance) may also impact their use of shared resources. Corvids may demonstrate aggressive behavior against other species when foraging if the overlap is high or avoid an area if another species is feeding [41]. Corvids also change their feeding preferences in larger flocks, indicating that interspecific relationships may impact resource use [107]. A study assessed four corvid species' segregation in using a refuse dump and found temporal (daily and seasonal) differentiation in its use by the different corvids [42]. Kleptoparasitism by the Carrion Crow against the other corvids was noted, which may have contributed to the temporal segregation in using this shared resource [42].

Since our study was conducted during the breeding season only, and some corvids (i.e., the Rook and Eurasian Jay) were shown to utilize urban areas more often during the winter, we expect different levels of habitat niche overlap among the corvids during the winter season, especially as wintering birds were shown to be more generalist in their habitats than breeding birds [11,19,87–89]. Many corvids were previously found to use

urban areas for nocturnal roosting [14,17]. Our data collection was only conducted in the morning and focused on breeding corvids but future research could investigate corvid habitat use at different times of the day. Furthermore, other corvids that may be urbanized in Europe have not been reported in our study (i.e., the Common Raven of which we only had two observations that were then dropped) [19]. Thus, other factors than the conditions of our study may determine their presence [19].

5. Conclusions

We studied the distribution, habitat selection, and spatial and habitat niche overlap of five corvid species in sixteen European cities during the breeding season. We found that three corvids were quite spread and abundant (The Carrion/Hooded Crow, Western Jackdaw, and Eurasian Magpie), while two were less present (the Rook and Eurasian Jay). High habitat overlap has been observed among the five studied corvids. Although their habitats highly overlapped, the species still had some tendencies in their habitat selection. Three corvid species selected urban areas with open spaces (the Carrion/Hooded Crow, Rook, and Eurasian Magpie). The Eurasian Jay was linked to increased tree cover. The Western Jackdaw was negatively correlated to bare soil cover. Species with similar habitat selection had congruent distribution. Our results are not surprising since corvids are highly adaptable generalists expected to have broad niches and, therefore, overlap in their habitats and spaces [14,29]. We assume that other factors, to be investigated in future studies, may impact their sympatric relationships, habitat, and spatial overlap, such as the season, time of day, interspecific interactions, and dietary preferences and habits [40–42,95,107].

References

1. McDonald, R.I.; Mansur, A.V.; Ascensão, F.; Colbert, M.; Crossman, K.; Elmqvist, T.; Gonzalez, A.; Güneralp, B.; Haase, D.; Hamann, M.; et al. Research Gaps in Knowledge of the Impact of Urban Growth on Biodiversity. *Nat. Sustain.* **2020**, *3*, 16–24. [CrossRef]
2. Center for International Earth Science Information Network—CIESIN; Columbia University; International Food Policy Research Institute—IFPRI; The World Bank; Centro Internacional de Agricultura Tropical—CIAT. *Global Rural-Urban Mapping Project, Version 1 (GRUMPv1): Urban Extents Grid*; Palisades; NASA Socioeconomic Data and Applications Center (SEDAC): New York, NY, USA, 2011. [CrossRef]
3. United Nations—Department of Economic and Social Affairs—Population Division. *World Urbanization Prospects: The 2018 Revision*; United Nations: New York, NY, USA, 2019; ISBN 9789211483192.
4. Alberti, M.; Correa, C.; Marzluff, J.M.; Hendry, A.P.; Palkovacs, E.P.; Gotanda, K.M.; Hunt, V.M.; Apgar, T.M.; Zhou, Y. Global Urban Signatures of Phenotypic Change in Animal and Plant Populations. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 8951–8956. [CrossRef] [PubMed]
5. Grimm, N.B.; Faeth, S.H.; Golubiewski, N.E.; Redman, C.L.; Wu, J.; Bai, X.; Briggs, J.M. Global Change and the Ecology of Cities. *Science* **2008**, *319*, 756–760. [CrossRef] [PubMed]
6. Prugh, L.R.; Stoner, C.J.; Epps, C.W.; Bean, W.T.; Ripple, W.J.; Laliberte, A.S.; Brashares, J.S. The Rise of the Mesopredator. *Bioscience* **2009**, *59*, 779–791. [CrossRef]
7. McKinney, M.L. Urbanization as a Major Cause of Biotic Homogenization. *Biol. Conserv.* **2006**, *127*, 247–260. [CrossRef]
8. Clergeau, P.; Croci, S.; Jokimäki, J.; Kaisanlahti-Jokimäki, M.L.; Dinetti, M. Avifauna Homogenisation by Urbanisation: Analysis at Different European Latitudes. *Biol. Conserv.* **2006**, *127*, 336–344. [CrossRef]
9. McKinney, M.L.; Lockwood, J.L. Biotic Homogenization: A Few Winners Replacing Many Losers in the next Mass Extinction. *Trends Ecol. Evol.* **1999**, *14*, 450–453. [CrossRef]
10. Garcia-Porta, J.; Sol, D.; Pennell, M.; Sayol, F.; Kaliontzopoulou, A.; Botero, C.A. Niche Expansion and Adaptive Divergence in the Global Radiation of Crows and Ravens. *Nat. Commun.* **2022**, *13*, 2086. [CrossRef]
11. Matsyura, A.V.; Zimaroyeva, A.A.; Jankowski, K. Spatial Patterns of Seasonal Distribution of Corvidae (the Case of Urban Habitats). *Biosyst. Divers.* **2016**, *24*, 459–465. [CrossRef]
12. Preininger, D.; Schoas, B.; Kramer, D.; Boeckle, M. Waste Disposal Sites as All-You-Can Eat Buffets for Carrion Crows (*Corvus corone*). *Animals* **2019**, *9*, 215. [CrossRef]
13. Wang, Y.; Chen, S.; Jiang, P.; Ding, P. Black-Billed Magpies (*Pica pica*) Adjust Nest Characteristics to Adapt to Urbanization in Hangzhou, China. *Can. J. Zool.* **2008**, *86*, 676–684. [CrossRef]
14. Benmazouz, I.; Jokimäki, J.; Lengyel, S.; Juhász, L.; Kaisanlahti-Jokimäki, M.-L.; Kardos, G.; Paládi, P.; Kövér, L. Corvids in Urban Environments: A Systematic Global. *Animals* **2021**, *11*, 3226. [CrossRef]
15. Seed, A.; Emery, N.; Clayton, N. Intelligence in Corvids and Apes: A Case of Convergent Evolution? *Ethology* **2009**, *115*, 401–420. [CrossRef]
16. Sol, D.; Duncan, R.P.; Blackburn, T.M.; Cassey, P.; Lefebvre, L. Big Brains, Enhanced Cognition, and Response of Birds to Novel Environments. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 5460–5465. [CrossRef]
17. Božič, L. Numbers, Distribution and Nest Site Characteristics of Jackdaw *Corvus monedula* in Slovenia and Its Conservation Status. *Acrocephalus* **2016**, *37*, 123–150. [CrossRef]
18. Szala, K.; Dylewski, Ł.; Tobolka, M. Winter Habitat Selection of Corvids in an Urban Ecosystem. *Urban Ecosyst.* **2020**, *23*, 483–493. [CrossRef]
19. Jokimäki, J.; Kaisanlahti-Jokimäki, M.L.; Suhonen, J. Long-Term Winter Population Trends of Corvids in Relation to Urbanization and Climate at Northern Latitudes. *Animals* **2022**, *12*, 1820. [CrossRef]
20. Belaire, J.A.; Westphal, L.M.; Whelan, C.J.; Minor, E.S. Urban Residents' Perceptions of Birds in the Neighborhood: Biodiversity, Cultural Ecosystem Services, and Disservices. *Condor* **2015**, *117*, 192–202. [CrossRef]
21. Julian, K.G.; Eidson, M.; Kipp, A.M.; Weiss, E.; Petersen, L.R.; Miller, J.R.; Hinten, S.R.; Marfin, A.A. Early Season Crow Mortality as a Sentinel for West Nile Virus Disease in Humans, Northeastern United States. *Vector Borne Zoonotic Dis.* **2002**, *2*, 145–155. [CrossRef]
22. Pesendorfer, M.B.; Sillett, T.S.; Koenig, W.D.; Morrison, S.A. Scatter-Hoarding Corvids as Seed Dispersers for Oaks and Pines: A Review of a Widely Distributed Mutualism and Its Utility to Habitat Restoration. *Condor* **2016**, *118*, 215–237. [CrossRef]
23. Jiguet, F. The Fox and the Crow. A Need to Update Pest Control Strategies. *Biol. Conserv.* **2020**, *248*, 108693. [CrossRef] [PubMed]
24. Yoda, T. Managing Urban Crow Populations in Japan. *Hum.-Wildl. Interact.* **2019**, *13*, 439–446. [CrossRef]
25. Evans, K.L.; Newson, S.E.; Gaston, K.J. Habitat Influences on Urban Avian Assemblages. *Ibis* **2009**, *151*, 19–39. [CrossRef]
26. Jokimäki, J.; Kaisanlahti-Jokimäki, M.; Sorace, A.; Fernández-Juricic, E.; Rodriguez-Prieto, I.; Jimenez, M.D. Evaluation of the "Safe Nesting Zone" Hypothesis across an Urban Gradient: A Multi-scale Study. *Ecography* **2005**, *28*, 59–70. [CrossRef]
27. Jokimäki, J.; Huhta, E. Artificial Nest Predation and Abundance of Birds Along an Urban Gradient. *Condor* **2000**, *102*, 838–847. [CrossRef]
28. Madden, C.F.; Arroyo, B.; Amar, A. A Review of the Impacts of Corvids on Bird Productivity and Abundance. *Ibis* **2015**, *157*, 1–16. [CrossRef]

29. Marzluff, J.M.; Neatherlin, E. Corvid Response to Human Settlements and Campgrounds: Causes, Consequences, and Challenges for Conservation. *Biol. Conserv.* **2006**, *130*, 301–314. [CrossRef]

30. Baltensperger, A.P.; Mullet, T.C.; Schmid, M.S.; Humphries, G.R.W.; Kövér, L.; Huettmann, F. Seasonal Observations and Machine-Learning-Based Spatial Model Predictions for the Common Raven (*Corvus corax*) in the Urban, Sub-Arctic Environment of Fairbanks, Alaska. *Polar Biol.* **2013**, *36*, 1587–1599. [CrossRef]

31. Nakahara, T.; Kuroe, M.; Hasegawa, O.; Hayashi, Y.; Mori, S.; Eguchi, K. Nest Site Characteristics of the Newly Established Eurasian Magpie *Pica pica* Population in Hokkaido, Japan. *Ornithol. Sci.* **2015**, *14*, 99–109. [CrossRef]

32. Xu, Y.; Cao, Z.; Wang, B. Effect of Urbanization Intensity on Nest-Site Selection by Eurasian Magpies (*Pica pica*). *Urban Ecosyst.* **2020**, *23*, 1099–1105. [CrossRef]

33. Ciebiera, O.; Czechowski, P.; Morelli, F.; Piekarski, R.; Bocheński, M.; Chachulska-Serweta, J.; Jerzak, L. Selection of Urbanized Areas by Magpie *Pica pica* in a Medium Size City in Poland. *Animals* **2021**, *11*, 1738. [CrossRef]

34. Jokimäki, J.; Suhonen, J.; Vuorisalo, T.; Kövér, L.; Kaisanlahti-Jokimäki, M.L. Urbanization and Nest-Site Selection of the Black-Billed Magpie (*Pica pica*) Populations in Two Finnish Cities: From a Persecuted Species to an Urban Exploiter. *Landsc. Urban Plan.* **2017**, *157*, 577–585. [CrossRef]

35. Šálek, M.; Grill, S.; Riegert, J. Nest-Site Selection of an Avian Urban Exploiter, the Eurasian Magpie *Pica pica*, across the Urban-Rural Gradient. *J. Vertebr. Biol.* **2020**, *70*, 20086.1–20086.11. [CrossRef]

36. Morrison, M.L. The Habitat Sampling and Analysis Paradigm Has Limited Value in Animal Conservation: A Prequel. *J. Wildl. Manag.* **2012**, *76*, 438–450. [CrossRef]

37. Hutchinson, G.E. Concluding Remarks. *Cold Spring Harb. Symp. Quant. Biol.* **1957**, *22*, 145–159. [CrossRef]

38. Whittaker, R.H.; Levin, S.A.; Rootj, R.B. Niche, Habitat, and Ecotope. *Am. Nat.* **1973**, *107*, 321–338. [CrossRef]

39. Marko, P.B. Sympatry. In *Encyclopedia of Ecology*; Academic Press: Cambridge, MA, USA, 2008; pp. 3450–3458. [CrossRef]

40. Matsubara, H. Comparative Study of Territoriality and Habitat Use in Syntopic Jungle Crow (*Corvus macrorhynchos*) and Carrion Crow (*C. corone*). *Ornithol. Sci.* **2003**, *2*, 103–111. [CrossRef]

41. Waite, R.K. Sympatric Corvids: Effects of Social Behaviour, Aggression and Avoidance on Feeding. *Behav. Ecol. Sociobiol.* **1984**, *15*, 55–59. [CrossRef]

42. Baglione, V.; Canestrari, D. Kleptoparasitism and Temporal Segregation of Sympatric Corvids Foraging in a Refuse Dump. *Auk* **2009**, *126*, 566–578. [CrossRef]

43. Gianpasquale, C.; Alberto, M. The Occurrence and Density of Three Sympatric Corvids in a Mediterranean Agroecosystem Explained by Land Use. *J. Ornithol.* **2019**, *160*, 1133–1150. [CrossRef]

44. Rolando, A.; Giachello, P. Interspecific Coexistence in Corvids in an Alpine Valley of Northwestern Italy. *Bolletino Zool.* **1992**, *59*, 281–288. [CrossRef]

45. Bibby, C.J.; Burgess, N.D.; Hillis, D.M.; Hill, D.A.; Mustoe, S. *Bird Census Techniques*; Elsevier: Amsterdam, The Netherlands, 1992; ISBN 0120958317.

46. Voříšek, P.; Klvaňová, A.; Wotton, S.; Gregory, R.D. *A Best Practice Guide for Wild Bird Monitoring Schemes*; Royal Society for the Protection of Birds: Sandy, UK, 2008.

47. Liordos, V.; Jokimäki, J.; Kaisanlahti-Jokimäki, M.L.; Valsamidis, E.; Kontsiotis, V.J. Patch, Matrix and Disturbance Variables Negatively Influence Bird Community Structure in Small-Sized Managed Green Spaces Located in Urban Core Areas. *Sci. Total Environ.* **2021**, *801*, 149617. [CrossRef] [PubMed]

48. Suhonen, J.; Jokimäki, J.; Kaisanlahti-Jokimäki, M.-L.; Morelli, F.; Benedetti, Y.; Rubio, E.; Pérez-Contreras, T.; Sprau, P.; Tryjanowski, P.; Møller, A.P.; et al. Occupancy-Frequency Distribution of Birds in Land-Sharing and-Sparing Urban Landscapes in Europe. *Landsc. Urban Plan.* **2022**, *226*, 104463. [CrossRef]

49. Kéry, M.; Royle, J.A.; Schmid, H. Modeling Avian Abundance from Replicated Counts Using Binomial Mixture Models. *Ecol. Appl.* **2005**, *15*, 1450–1461. [CrossRef]

50. Callaghan, C.T.; Major, R.E.; Lyons, M.B.; Martin, J.M.; Kingsford, R.T. The Effects of Local and Landscape Habitat Attributes on Bird Diversity in Urban Greenspaces. *Ecosphere* **2018**, *9*, e02347. [CrossRef]

51. Chace, J.F.; Walsh, J.J. Urban Effects on Native Avifauna: A Review. *Landsc. Urban Plan.* **2006**, *74*, 46–69. [CrossRef]

52. Liordos, V.; Jokimäki, J.; Kaisanlahti-Jokimäki, M.-L.; Valsamidis, E.; Kontsiotis, V.J. Niche Analysis and Conservation of Bird Species Using Urban Core Areas. *Sustainability* **2021**, *13*, 6327. [CrossRef]

53. Muñoz-Pedreros, A.; González-Urrutia, M.; Encina-Montoya, F.; Norambuena, H.V. Effects of Vegetation Strata and Human Disturbance on Bird Diversity in Green Areas in a City in Southern Chile. *Avian Res.* **2018**, *9*, 38. [CrossRef]

54. Peris, S.; Montelongo, T. Birds and Small Urban Parks: A Study in a High Plateau City. *Turk. J. Zool.* **2014**, *38*, 316–325. [CrossRef]

55. Amaya-Espinel, J.D.; Hostetler, M.; Henríquez, C.; Bonacic, C. The Influence of Building Density on Neotropical Bird Communities Found in Small Urban Parks. *Landsc. Urban Plan.* **2019**, *190*, 103578. [CrossRef]

56. Miller, S.G.; Knight, R.L.; Miller, C.K. Wildlife Responses to Pedestrians and Dogs. *Wildl. Soc. Bull.* **2001**, *29*, 124–132.

57. Adams, C.A.; Blumenthal, A.; Fernández-Juricic, E.; Bayne, E.; St Clair, C.C. Effect of Anthropogenic Light on Bird Movement, Habitat Selection, and Distribution: A Systematic Map Protocol. *Environ. Evid.* **2019**, *8*, 13. [CrossRef]

58. Ciach, M.; Fröhlich, A. Habitat Type, Food Resources, Noise and Light Pollution Explain the Species Composition, Abundance and Stability of a Winter Bird Assemblage in an Urban Environment. *Urban Ecosyst.* **2017**, *20*, 547–559. [CrossRef]

59. Francis, C.D.; Ortega, C.P.; Cruz, A. Noise Pollution Changes Avian Communities and Species Interactions. *Curr. Biol.* **2009**, *19*, 1415–1419. [CrossRef]
60. Morelli, F.; Benedetti, Y.; Ibáñez-Álamo, J.D.; Tryjanowski, P.; Jokimäki, J.; Kaisanlahti-Jokimäki, M.-L.; Suhonen, J.; Díaz, M.; Møller, A.P.; Moravec, D.; et al. Effects of Urbanization on Taxonomic, Functional and Phylogenetic Avian Diversity in Europe. *Sci. Total Environ.* **2021**, *795*, 148874. [CrossRef]
61. Parkin, D.T.; Collinson, M.; Helbig, A.J.; Knox, A.G.; Sangster, G. The Taxonomic Status of Carrion and Hooded Crows. *Br. Birds* **2003**, *96*, 274–290.
62. Vrezec, A. Historical Occurrence of the Hooded/Carrion Crow (*Corvus cornix/corone*) in Urban Areas of Europe with Emphasis on Slovenia. *Annales Ser. Hist. Nat.* **2010**, *20*, 131–140.
63. Keller, V.; Herrando, S.; Voríšek, P.; Franch, M.; Kipson, M.; Milanesi, P.; Martí, D.; Anton, M.; Klvanová, A.; Kalyakin, M.V. *European Breeding Bird Atlas 2: Distribution, Abundance and Change*; Lynx Edicions: Cerdanyola del Vallès, Spain, 2020; ISBN 8416728380.
64. Pearman, P.B.; Lavergne, S.; Roquet, C.; Wüest, R.; Zimmermann, N.E.; Thuiller, W. Phylogenetic Patterns of Climatic, Habitat and Trophic Niches in a European Avian Assemblage. *Glob. Ecol. Biogeogr.* **2014**, *23*, 414–424. [CrossRef]
65. Storchová, L.; Hořák, D. Life-History Characteristics of European Birds. *Glob. Ecol. Biogeogr.* **2018**, *27*, 400–406. [CrossRef]
66. Metzler, D.; Knief, U.; Peñalba, J.V.; Wolf, J.B.W. Assortative Mating and Epistatic Mating-Trait Architecture Induce Complex Movement of the Crow Hybrid Zone. *Evolution* **2021**, *75*, 3154–3174. [CrossRef]
67. Wolf, J.B.W.; Bayer, T.; Haubold, B.; Schilhabel, M.; Rosenstiel, P.; Tautz, D. Nucleotide Divergence vs. Gene Expression Differentiation: Comparative Transcriptome Sequencing in Natural Isolates from the Carrion Crow and Its Hybrid Zone with the Hooded Crow. *Mol. Ecol.* **2010**, *19*, 162–175. [CrossRef] [PubMed]
68. Knief, U.; Bossu, C.M.; Saino, N.; Hansson, B.; Poelstra, J.; Vijay, N.; Weissensteiner, M.; Wolf, J.B.W. Epistatic Mutations under Divergent Selection Govern Phenotypic Variation in the Crow Hybrid Zone. *Nat. Ecol. Evol.* **2019**, *3*, 570–576. [CrossRef] [PubMed]
69. Mantel, N. The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer Res.* **1967**, *27*, 209–220. [PubMed]
70. Dray, S.; Dufour, A. The Ade4 Package: Implementing the Duality Diagram for Ecologists. *J. Stat. Softw.* **2007**, *22*, 1–20. [CrossRef]
71. Lysy, M.; Stasko, A.D.; Swanson, H.K. Package 'NicheROVER' Niche Region and Niche Overlap Metrics for Multidimensional Ecological Niches. 2021. Available online: https://CRAN.R-project.org/package=nicheROVER (accessed on 7 June 2021).
72. Swanson, H.K.; Lysy, M.; Power, M.; Stasko, A.D.; Johnson, J.D.; Reist, J. Ecological Niches and Niche Overlap R Eports. *Ecology* **2015**, *96*, 318–324. [CrossRef]
73. Escoriza, D.; Amat, F. Habitat Partitioning and Overlap by Large Lacertid Lizards in Southern Europe. *Diversity* **2021**, *13*, 155. [CrossRef]
74. Bates, D.; Maechler, M.; Bolker, B.; Walker, S. Lme4: Linear Mixed-Effects Models Using Eigen and S4—R Package 2014. *arXiv* **2014**, arXiv:1406.5823.
75. Barton, K. MuMIn: Multi-Model Inference. R Package Version 1.15.1. 2020. Available online: http://CRAN.R-project.org/package=MuMIn (accessed on 7 June 2021).
76. Burnham, K.P.; Anderson, D.R. *Model Selection and Multimodel Inference*, 2nd ed.; Springer: New York, NY, USA, 2002.
77. R Development Core Team. *R: A Language and Environment for Statistical Computing Version 4.0.3*; R Foundation for Statistical Computing: Vienna, Austria, 2020.
78. François, C.; Alexandre, L.; Julliard, R. Effects of Landscape Urbanization on Magpie Occupancy Dynamics in France. *Landsc. Ecol.* **2008**, *23*, 527–538. [CrossRef]
79. Wang, Z.; Wang, Y.; Jerzak, L.; Zhang, Z. Nest Site Selection of the Magpie *Pica pica* Sericea in Beijing of China. *Stud. Biol.* **2010**, *4*, 71–82. [CrossRef]
80. Jokimäki, J.; Suhonen, J. Distribution and Habitat Selection of Wintering Birds in Urban Environments. *Landsc. Urban Plan.* **1998**, *39*, 253–263. [CrossRef]
81. Jerzak, L. *Synurbizacja sroki Pica pica w Eurazji*; Uniwersytet Zielonogórski: Zielona Góra, Poland, 2002.
82. Czechowski, P.; Bocheński, M.; Ciebiera, O. Decline Of Jackdaws *Corvus monedula* In The City Of Zielona Góra. *Int. Stud. Sparrows* **2013**, *37*, 32–36. [CrossRef]
83. Salvati, L. Nest Site and Breeding Habitat Characteristics in Urban Jackdaws *Corvus monedula* in Rome (Italy). *Acta Ornithol.* **2002**, *37*, 15–19. [CrossRef]
84. Meyrier, E.; Jenni, L.; Bötsch, Y.; Strebel, S.; Erne, B.; Tablado, Z. Happy to Breed in the City? Urban Food Resources Limit Reproductive Output in Western Jackdaws. *Ecol. Evol.* **2017**, *7*, 1363–1374. [CrossRef]
85. Vuorisalo, T.; Andersson, H.; Hugg, T.; Lahtinen, R.; Laaksonen, H.; Lehikoinen, E. Urban Development from an Avian Perspective: Causes of Hooded Crow (*Corvus corone cornix*) Urbanisation in Two Finnish Cities. *Landsc. Urban Plan.* **2003**, *62*, 69–87. [CrossRef]
86. The European Red List of Birds. Luxembourg: Publications Office of the European Union. *Birdlife Int.* **2021**, *28*, 3–19.
87. Jadczyk, P.; Drzeniecka-Osiadacz, A. Feeding Strategy of Wintering Rooks *Corvus frugilegus* L. in Urban Habitats. *Pol. J. Ecol.* **2013**, *61*, 587–596.
88. Obukhova, N.Y. Nesting Dynamics of Corvids (Corvidae) in the City of Moscow and Moscow Oblast. *Biol. Bull.* **2018**, *45*, 1096–1105. [CrossRef]

89. Zimaroyeva, A.A.; Matsyura, A.V.; Jankowski, K. Spatial Patterns of Habitat Distribution of Corvidae (the Case of Urban-Rural Gradient). *Biosyst. Divers.* **2016**, *24*, 451–458. [CrossRef]

90. Díaz, M. Food Choice by Seed-Eating Birds in Relation to Seed Chemistry. *Comp. Biochem. Physiol. Part A Physiol.* **1996**, *113*, 239–246. [CrossRef]

91. Andersson, M.; Wallander, J.; Isaksson, D. Predator Perches: A Visual Search Perspective. *Funct. Ecol.* **2009**, *23*, 373–379. [CrossRef]

92. Fernández-Juricic, E.; Blumstein, D.T.; Abrica, G.; Manriquez, L.; Adams, L.B.; Adams, R.; Daneshrad, M.; Rodriguez-Prieto, I. Relationships of Anti-Predator Escape and Post-Escape Responses with Body Mass and Morphology: A Comparative Avian Study. *Evol. Ecol. Res.* **2006**, *8*, 731–752.

93. Tzortzakaki, O.; Kati, V.; Kassara, C.; Tietze, D.T.; Giokas, S. Seasonal Patterns of Urban Bird Diversity in a Mediterranean Coastal City: The Positive Role of Open Green Spaces. *Urban Ecosyst.* **2018**, *21*, 27–39. [CrossRef]

94. Mason, C.F.; Macdonald, S.M. Distribution of Foraging Rooks, Corvus frugilegus, and Rookeries in a Landscape in Eastern England Dominated by Winter Cereals. *Folia Zool.* **2004**, *53*, 179–188.

95. Waite, R.K. Winter Habitat Selection and Foraging Behaviour in Sympatric Corvids. *Ornis Scand.* **1984**, *15*, 55–62. [CrossRef]

96. Zmihorski, M.; Halba, R.; Mazgajski, T.D. Long-Term Spatio-Temporal Dynamics of Corvids Wintering in Urban Parks of Warsaw, Poland. *Ornis Fenn.* **2010**, *87*, 61–68.

97. Pons, J.; Pausas, J.G. Modelling Jay (Garrulus Glandarius) Abundance and Distribution for Oak Regeneration Assessment in Mediterranean Landscapes. *For. Ecol. Manag.* **2008**, *256*, 578–584. [CrossRef]

98. Mazgajski, T.D.; Zmihorski, M.; Halba, R.; Woźniak, A. Long-Term Population Trends of Corvids Wintering in Urban Parks in Central Poland. *Pol. J. Ecol.* **2008**, *56*, 521–526.

99. Sorace, A.; Gustin, M. Distribution of Generalist and Specialist Predators along Urban Gradients. *Landsc. Urban Plan.* **2009**, *90*, 111–118. [CrossRef]

100. Bossema, I. Jays and Oaks: An Eco-Ethological Study of a Symbiosis. *Behaviour* **1979**, *70*, 1–116. [CrossRef]

101. Morán-López, T.; Alonso, C.L.; Díaz, M. Landscape Effects on Jay Foraging Behavior Decrease Acorn Dispersal Services in Dehesas. *Acta Oecologica* **2015**, *69*, 52–64. [CrossRef]

102. Fischer, J.D.; Cleeton, S.H.; Lyons, T.P.; Miller, J.R. Urbanization and the Predation Paradox: The Role of Trophic Dynamics in Structuring Vertebrate Communities. *Bioscience* **2012**, *62*, 809–818. [CrossRef]

103. Evans, K.L.; Hatchwell, B.J.; Parnell, M.; Gaston, K.J. A Conceptual Framework for the Colonisation of Urban Areas: The Blackbird Turdus Merula as a Case Study. *Biol. Rev.* **2010**, *85*, 643–667. [CrossRef]

104. Tobias, J.A.; Ottenburghs, J.; Pigot, A.L. Avian Diversity: Speciation, Macroevolution, and Ecological Function. *Annu. Rev. Ecol. Evol. Syst.* **2020**, *51*, 533–560. [CrossRef]

105. Moi, D.A.; García-Ríos, R.; Hong, Z.; Daquila, B.V.; Mormul, R.P. Intermediate Disturbance Hypothesis in Ecology: A Literature Review. *Ann. Zool. Fenn.* **2020**, *57*, 67–78. [CrossRef]

106. Kulemeyer, C.; Asbahr, K.; Gunz, P.; Frahnert, S.; Bairlein, F. Functional Morphology and Integration of Corvid Skulls—A 3D Geometric Morphometric Approach. *Front. Zool.* **2009**, *6*, 2. [CrossRef]

107. Rolando, A. Data on Eco-Ethology of Coexistence in Corvids in North-Western Italy. *Bolletino Zool.* **1988**, *55*, 315–321. [CrossRef]

Annex II. Urban noise slows down the antipredator reaction of Eurasian Magpies.

Farah Abou-Zeid*, Yanina Benedetti, Anastasiia Siretckaia, Federico Morelli, 2024.

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Urban noise slows down the antipredator reaction of Eurasian Magpies

Farah Abou-Zeid[1]*, Yanina Benedetti[1], Anastasiia Siretckaia[1] and Federico Morelli[1,2]

[1]Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Praha, Czechia,
[2]Institute of Biological Sciences, University of Zielona Góra, Zielona Góra, Poland

Urban areas are known to have high levels of noise pollution, which can impact an animal's antipredator behavior. Noise can either distract the animal or mask the sounds of a predator, increasing the animal's vulnerability to predation. However, the prey may increase vigilance in noisier environments, thus reducing energy and time spent on other activities. Alert Distance (AD) refers to the distance at which an animal becomes alert to a potential predator approaching. Flight Initiation Distance (FID) is the distance from the potential predator at which the animal flees. We studied the impact of ambient noise pollution on the AD and a corrected FID (FID/AD) of Eurasian Magpies (*Pica pica*) using a field investigator as a potential predator walking towards birds at a constant speed. We found that the noise level did not affect the AD. Still, noise had a negative effect on the Eurasian Magpies' FID/ADs, suggesting that noise may slow their reaction to a potential threat but not their ability to detect it. Thus, our research highlights that urban noise pollution can increase an individual's vulnerability to predation, even when predators are still detectable. Ambient noise may distract the bird by diverting some of its limited attention and causing a delayed response to the predators. Alternatively, noise could be masking auditory cues that would have otherwise been added together with visual cues to cause an enhanced response. More research is necessary to understand the effects of noise pollution on the antipredator behavior of birds in urban areas, taking into account the specific strategies and adaptations of each species.

KEYWORDS

flight initiation distance, alert distance, Pica pica, alertness, escape behavior, threat detection, vigilance

1 Introduction

Urban areas are filled with anthropogenic sounds from traffic, industrial, and commercial activities (Warren et al., 2006). Sounds are not inherently problematic, as most animals use them for communication and survival (Sun and Narins, 2005; Sordello et al., 2020). However, after a certain threshold, human-made sounds begin to

cause disruptions to wildlife and, thus, turn into "noise pollution" (Sordello et al., 2020). The extent of disturbance is relative and varies based on species tolerance levels (Sordello et al., 2020). Noise pollution may interfere with wildlife by masking their natural sounds, affecting communication and essential auditory signals crucial for survival (Sun and Narins, 2005; Slabbekoorn and Ripmeester, 2008; Barber et al., 2010). Additionally, noise has been observed to elevate stress levels in numerous animal species, leading to complex and diverse implications for their physiological systems (Kight and Swaddle, 2011).

Birds are an example of fauna adversely affected by noise, as they rely on acoustic communication and signals to interact with their environment (Francis et al., 2009; Hu and Cardoso, 2009; Petrelli et al., 2017). Birds use their songs to communicate with mates, brood, and conspecifics, attract partners, and establish dominance (Catchpole and Slater, 2003; Slabbekoorn and Ripmeester, 2008). Auditory cues also serve birds to detect approaching predators and send and receive signals to and from their conspecifics about predation threats (Hollén and Radford, 2009). Birds are considered model organisms in urban ecology and good indicators of habitat quality as they are easy to spot and study and are responsive to anthropogenic habitat alterations (Marzluff, 2008; Croci et al., 2008).

Intense ambient noise may impact an animal's antipredator behavior in various ways (Shannon et al., 2016). On the one hand, noise may hinder the individual's ability to detect threats (either by masking auditory cues of the predator or by distracting the prey; Barber et al., 2010; Chan et al., 2010a; Zhou et al., 2019), increasing the predation threat for the animal (Chan et al., 2010a; Chan et al., 2010b). On the other hand, noise may lead the animal to augment its vigilance (as an attempt to compensate for its compromised hearing or by perceiving the noise as a direct threat in itself; Meillère et al., 2015; Kern and Radford, 2016; Shannon et al., 2016; Evans et al., 2018). However, increased vigilance would entail additional energy costs and keep the animal from optimal foraging and other activities (Kern and Radford, 2016). Thus, urban noise may disturb an animal's antipredator behavior in two opposing, unfavorable manners.

Several studies investigated the impacts of noise pollution on the antipredator behavior of birds (Gravolin et al., 2014; Meillère et al., 2015; Petrelli et al., 2017; Evans et al., 2018; Zhou et al., 2019; Merrall and Evans, 2020). Various methods were used, such as observing vigilant behavior (Evans et al., 2018), willingness to visit feeders (Merrall and Evans, 2020), response to alarm calls (Zhou et al., 2019), and others. Few have used the Flight Initiation Distance (hereafter FID; Gravolin et al., 2014; Meillère et al., 2015; Petrelli et al., 2017).

FID is among the most widely investigated antipredator behaviors used extensively in behavioral ecology studies to assess fear, risk-taking, evolution, or adaptation (Møller, 2021). FID is the distance from an advancing danger (usually a researcher approaching the animal under standard conditions) that leads an animal to flee (Blumstein, 2003). Alert Distance (hereafter AD) is the distance before FID, at which the animal becomes aware of the predator and actively observes it before fleeing (Fernández-Juricic et al., 2001). The FID must compromise between flight costs and benefits to stay put and resume current activity (Møller, 2008). For example, in urban areas, where humans are commonly around, energetically costly constant fleeing would put birds at a disadvantage at the expense of optimal foraging (Cooper and Frederick, 2007). Thus, urban birds have lower fear responses than their rural counterparts and prioritize investing their energy in other activities, such as foraging and reproducing (Cooper and Frederick, 2007; Tryjanowski et al., 2016; Morelli et al., 2019; Díaz et al., 2021). They save energy by delaying flight and actively monitoring the predator until the costs of remaining put are higher than those of fleeing current activity (Price, 2008).

Although a few studies investigated the impacts of noise pollution on the FID of birds (Meillère et al., 2015; Petrelli et al., 2017), no study has also studied its impact on AD (but see Shannon et al., 2016 in a study on Prairie Dogs; *Cynomys ludovicianus*). Most studies do not account for AD and use FID as a proxy for the animals' capacity to detect danger since the two are highly correlated (Blumstein et al., 2005). However, we hypothesize that high levels of noise pollution may have different impacts on the alertness and antipredator response of animals and that FID alone may not be sufficient to reflect the effects of noise on the attention of individuals. For example, noise may reduce the birds' capacity to perceive the sounds of approaching predators (Barber et al., 2010; Chan et al., 2010b; Zhou et al., 2019), leading to a lower AD. However, birds exposed to more noise may be more stressed, leading them to flee sooner after they detect the danger, as shown in previous studies (Meillère et al., 2015).

Therefore, we think it is valuable to study the impacts of urban noise on AD and FID in a bird study regarding noise pollution, which has not yet been done to our knowledge. This approach may highlight two opposing ways urban noise may impact an animal's antipredator behavior (either by distracting the animal or causing it to increase its vigilance) that are not mutually exclusive.

Many corvid species, including the Eurasian Magpie (*Pica pica*), have spread into urban areas (Benmazouz et al., 2021; Abou Zeid et al., 2023). Their behavioral flexibility has allowed them to adapt to urban areas by modifying their behavior (Benmazouz et al., 2021). For example, Eurasian Magpies tend to raise the heights of their nests in trees as urbanization intensity increases to avoid disturbances from humans and predation from Hooded Crows (*Corvus cornix*; Šálek et al., 2020; Xu et al., 2020; Ciebiera et al., 2021). Thus, Eurasian Magpies are ideal subjects for studying urban noise's ecological implications on animal behavior.

This study aims to investigate the effect of noise pollution on Eurasian Magpies' antipredator behavior in urban areas during the breeding season. The specific objectives are 1) to study the variation of AD and FID/AD of Eurasian Magpies across a gradient of urban noise and 2) to investigate the consistency of the impact of noise on threat detection and speed of the escape response. We hypothesize two potential reactions of Eurasian Magpies against increased noise: a) reduction in the birds' AD due to masking or distraction or b) increase in AD due to heightened vigilance. Additionally, we expect that FID/AD may be increased so the Eurasian Magpies can compensate for reduced hearing by reacting more quickly to perceived threats. We think noise's impact on threat detection may not be congruent with the escape response, even though the

two may be highly correlated. To investigate these hypotheses, we modeled the effect of ambient noise on the AD and FID/AD of Eurasian Magpies in Prague, taking into account other confounding variables, such as the Starting Distance (hereafter SD, the distance that separates the researcher from the bird at the start of the sampling), the age of the individual, and the site surveyed.

2 Methods

2.1 Study area and field data collection

The fieldwork was conducted in Prague, Czechia, during the breeding season of 2022 (with more than 95% of data collected from mid-May until mid-July and before noon). Public parks and green areas with large Eurasian Magpie populations were surveyed on days that were not rainy or strongly windy (Beauford number ≤ 3). Standardized AD and FID collection methods were used (Blumstein, 2003). Only Eurasian Magpie individuals who were on the ground were sampled. When an individual was detected, the field researcher (FAZ, wearing similar inconspicuous dark clothes) began the collection by dropping a small marker (made of cotton and cloth not to attract the bird's attention) behind their back to mark the Starting Distance (SD). The researcher began approaching the bird slowly and at a steady speed. Another marker was dropped when the bird started to exhibit alert behavior to the advancing person (looking at the field investigator, displaying cautious behavior, turning its head, etc.; Fernández-Juricic et al., 2001). A third marker was dropped when the bird escaped (by jumping or flying). Then, the researcher would stand in the bird's last occupied spot and collect information regarding the noise level. The ambient noise level (dBA) was measured using a Multifunctional environment meter 13/464/0 from Brannan by collecting the minimum and maximum noise levels detected by the tool in 1 minute right after each individual was approached. The mean noise level was calculated as the average of the maximum and minimum collected within the minute. This was done to ensure that measured noise reflected the noise levels when the individual was approached. We also took note of the individual's age (juvenile vs. adult). Juveniles were identified by smaller body sizes and shorter tails. Additionally, we counted all Eurasian Magpies in the flock near the sampled individual and the density of people present within a radius of 50 meters around the sampling point. After taking note of all these variables, the investigator measured the SD, AD, and FID from the birds' last perch to the respective marker using a surveyor's tape. We did not approach individuals who were alert before the start of the collection (Morelli et al., 2022). To reduce pseudo-replication bias, we avoided resampling the same individuals. Sites (parks or other green areas) with only one observation were also dropped.

2.2 Statistical analyses

We calculated the ratio of FID to AD (FID/AD). Since the maximum distance the individual can take flight at is constrained by the AD, it is necessary to use a corrected flight distance (Shannon et al., 2016). Several authors have used the distance separating AD and FID (AD – FID) as a corrected flight distance (also termed Buffer Distance or Assessment Interval; Fernández-Juricic et al., 2002; Shannon et al., 2016; Tätte et al., 2019). However, calculating the corrected flight distance in this way gives an absolute number and does not relay the relationship between FID and AD. Therefore, a better way to adjust FID for AD is to look at the proportions (FID/AD). We used the FID/AD ratio as a corrected flight response measure. High FID/AD indicates a small difference between FID and AD, suggesting a fast escape after threat detection. In contrast, smaller FID/AD shows a larger difference between the two measures and, thus, a slower escape after threat detection.

SD and AD were root square transformed to approach a normal distribution. All continuous variables were scaled and centered. Pearson's correlation coefficients were calculated to check the correlation among the SD and AD and SD and FID/AD measures.

Generalized Linear Mixed Models (hereafter GLMMs) were performed to assess the impact of ambient urban noise on the Eurasian Magpies' AD and FID/AD. AD and FID/AD were the response variables, while the mean noise level was the predictor. The age of the individual (juvenile or adult) and the SD were also predictors, as they were previously demonstrated to impact the antipredator responses of birds (Blumstein, 2003; Kalb et al., 2019). Since all data was collected in Prague, we can assume a similar predation risk across the collected data. Additionally, the site (or park) was used as a random factor to reduce confounding variables (such as the variability among human activity in different sites and the type of vegetation cover), which may impact the antipredator behavior (Radvan et al., 2023).

Since most Eurasian Magpies sampled were alone or in very small flocks (93% of sampled individuals had two or fewer conspecifics nearby), we have not included the flock size in the models. Similarly, we have not included the human density around the sampled individuals since human density was similar across observations, with 75% of observations having five or fewer people within a 50 m radius around the sampled individual.

The models were fit using the R package "lme4" (Bates et al., 2014). The R package "lmerTest" was used to derive p-values using Satterthwarte's degrees of freedom method (Kuznetsova et al., 2017). The Variation Inflation Factor (VIF) was calculated from the "car" package to assess multicollinearity among the predictors, but none was detected (all VIF < 5; Fox et al., 2007). Plots of residuals against fitted values were evaluated visually for further model validation. Cook's distance values were used to detect influential observations, but none were found. The conditional R^2 (the proportion of variance explained by fixed and random effects and marginal R^2 (the ratio of variance presented by the fixed effects only) were calculated to explore the models' performance using the r2 function from the 'performance' package of R (Lüdecke et al., 2021)

All analyses were performed using R software version 4.3.0 (R Core Team, 2022).

3 Results

Initially, we sampled 169 Eurasian Magpie individuals at 13 different sites. After removing sites with single observations, 167 individuals remained (138 adults and 29 juveniles) at 11 sites. On average, around 6 Eurasian Magpies were sampled in one session. Mean ambient sound levels ranged from 43.0 to 63.2 dBA, averaging 50.4 ± 5.1 (SD) dBA. Min noise ranged from 38.0 to 56.7 and averaged 44.9 ± 4.1 dBA. Max noise ranged from 45.6 to 77.0, averaging 55.9 ± 7.2 dBA. The average SD, AD, and FID/AD values for adults, juveniles, and all data are presented in Table 1.

SD and AD were positively correlated ($r_{(165)}$ = 0.84, p-value < 0.001; Figure 1). SD was negatively correlated with the FID/AD ratio ($r_{(165)}$ = -0.37, p-value < 0.001; Figure 1).

As for the results of the GLMMs the SD had a significant positive impact on the AD (Table 2); juveniles had significantly longer ADs than adults (Table 2). The noise level did not show a significant effect on the AD of the Eurasian Magpies (Table 2). The SD and noise levels had a significant negative effect on the FID/AD ratio, while the age did not seem to have any (Table 3; Figure 2).

4 Discussion

Surviving predation attempts requires efficiently detecting predators and assessing their danger level (Lukas et al., 2021). Here, we studied the impacts of ambient urban noise on Eurasian Magpies' alertness to predators and antipredator response through AD and FID/AD under a gradient of urban noise. We found no significant effect of noise on AD, but increased noise negatively impacted the Eurasian Magpies' FID/AD ratios.

4.1 Noise and alertness

We found no impact of the ambient noise levels on the AD of the Eurasian Magpies surveyed. Several studies have shown that many birds (especially ground foraging species) spend more time vigilant and visually scanning for predators in noisier environments and less time feeding to compensate for their reduced hearing abilities (Quinn et al., 2006; Ware et al., 2015; Klett-Mingo et al., 2016; Partan, 2017; Evans et al., 2018). We had predicted that such an increase in vigilance might lead to a rise in the ADs of the Eurasian Magpies. Tätte et al. (2019) found that although birds in urban areas were more vigilant (assessed by the proxy of the head-raising behavior of birds), there was no correlation between the

increase in vigilance and the detection of predators (AD). Some birds may be able to detect threats while foraging with their heads down due to their wide visual field, making them less reliant on sound cues, and thus, they may not need to compensate for reduced hearing by increasing vigilance (Lima and Bednekoff, 1999; Blumstein et al., 2004; Fernández-Juricic et al., 2004). However, this also means that those birds may detect a predator before displaying vigilant behavior or looking directly at it, which is the criteria for measuring AD (Blumstein et al., 2004). Therefore, we can not entirely deny the possible impact of noise pollution on the Eurasian Magpies' capacity to detect danger. Still, there seems to be no variation in their displayed vigilant behavior. The noise may still impact the predator detection capacity of the Eurasian Magpies, but it could need larger samples to confirm or a different technique to assess (Blumstein et al., 2004).

4.2 Noise and escape

Although the Eurasian Magpies did not seem to have modified alertness, they responded more slowly to threats and had significantly smaller FID/AD ratios under noisier conditions. Meillère et al. (2015) found an opposite trend in breeding female House Sparrows (*Passer domesticus*). However, the birds were rural birds that were exposed to chronic noise for only two months, while in our study, the Eurasian Magpies surveyed are urban individuals that have been exposed to urban noise longer and have adapted to the presence of humans in urban parks and may view them as less of a threat than the rural House Sparrows. In addition, different species may react differently to noise. Another study found a negative correlation between the level of noise and the FID of ground foraging bird species, indicating a delayed escape, similar to our results, but found a different trend in flycatching and canopy-gleaning species (Petrelli et al., 2017). Therefore, the impact of noise pollution on the antipredator behavior of birds may be species-specific. A similar pattern to our study was discovered in a non-avian species, the Caribbean Hermit Crab (*Coenobita clypeatus*), which was slower to respond to simulated images of a silent predator when exposed to noise and the authors suggested the distracted prey hypothesis (Chan et al., 2010a; Chan et al., 2010b). Since individuals have limited attention, they must divide it among relevant stimuli and processes (i.e., foraging and vigilance; Dukas, 2004; Washburn and Taglialatela, 2006). Additional stimuli, such as anthropogenic noise, may distract an animal by causing it to involuntarily shift some of its limited attention to it and away from the relevant tasks at hand, which would increase its vulnerability to predation (Dukas, 2004; Chan et al., 2010b). Increased noise may also be related to increased traffic or human presence, which could create additional simultaneous visual distractions to which the bird may be diverting some of its attention. Here, we also measured the AD to confirm whether the impact of noise on the escape behavior can also reflect the alertness levels of the individuals. We found no noise effect on the Eurasian Magpies' AD. Therefore, our results do not directly support the distracted prey hypothesis in terms of their capacity to detect the predator. The Eurasian Magpies studied may have taken longer to

TABLE 1 The mean Starting Distance (SD), Alert Distance (AD), and Flight Initiation Distance (FID)/AD ± Standard Deviation for adults, juveniles, and all Eurasian Magpie individuals.

	SD (m)	AD (m)	FID/AD
Adults (n=138)	33.71 ± 13.04	25.26 ± 10.40	0.57 ± 0.23
Juveniles (n=29)	33.32 ± 9.10	28.02 ± 8.88	0.58 ± 0.18
All data (n=167)	33.64 ± 12.42	25.74 ± 10.19	0.57 ± 0.22
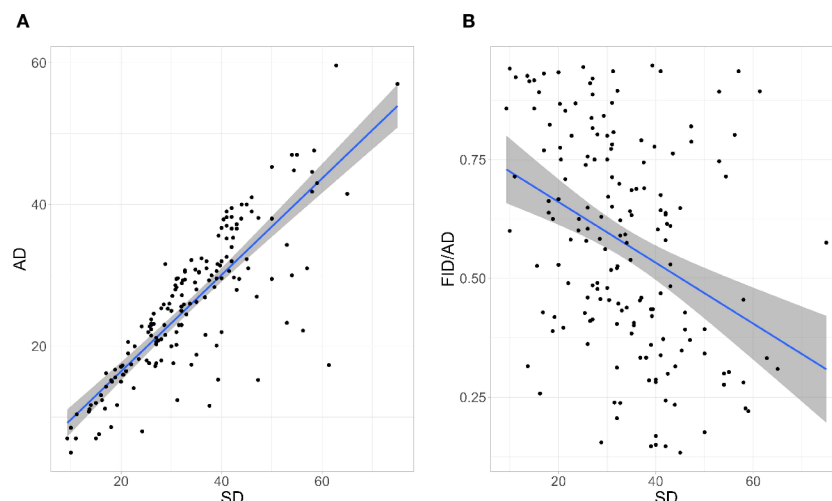
FIGURE 1
The correlation between **(A)** Alert Distance (AD) and Starting Distance (SD) and **(B)** SD and the Flight Initiation Distance/Alert Distance (FID/AD) ratio of Eurasian Magpies surveyed. Envelopes around linear regression lines represent the 95% Confidence Intervals. n = 167.

assess the level of threat the approaching person poses due to their attention being divided among several tasks and their brain processes being overwhelmed at increased noise levels. In this case, it could be that the noise is not interfering with their capacity to receive visual stimuli from the predator but rather distracting and slowing down their decision-making process or execution of their response (Dukas, 2002). Tätte et al. (2019) found that birds in urban areas were more vigilant but delayed their escape after detecting the threat and suggested that the increased distractions in urban areas, including noise, may explain their results (Chan et al., 2010b). Our study supports their suggestion as Eurasian Magpies took longer to assess threat as background noise increased.

Another non-mutually exclusive explanation could be that the background noise may be masking relevant auditory cues, such as the footfalls of the approaching predator (Barber et al., 2010; Zhou et al., 2019). Although the Eurasian Magpies still seem to detect the predator normally, their perception of auditory cues may be impaired under higher noise. Animals resort to multisensory integration to lessen environmental uncertainty (Munoz and Blumstein, 2012; Partan, 2017). Multisensory integration relies on different stimuli from several sensory modalities during decision-making, such as during antipredator

behavior (Munoz and Blumstein, 2012). Stimuli are considered "redundant" if they lead to a similar response in the same direction (i.e., escaping the threat; Partan et al., 2009). When presented together, redundant stimuli interact, leading to three possible behaviors of the recipient: equivalence (response is not different from when stimuli are presented alone), enhancement (response is more intense), and antagonism (response is reduced; Partan and Marler, 2005; Munoz and Blumstein, 2012). At lower noise, the Eurasian Magpies would receive auditory and visual cues from the predator, which may lead to an enhanced response and cause them to flee faster from farther distances than Eurasian Magpies approached at noisier conditions. In other avian and non-avian studies, visual and auditory cues were shown to lead to an enhanced antipredator response. For example, Free-living Hoatzins (*Opisthocomus hoazin*) were more alert and escaped more quickly when approached by loud tourists than silent ones (Karp and Root, 2009). In addition, when combined, auditory and visual cues of predators instigated stronger and faster antipredator responses from a fish species when presented separately (Lukas et al., 2021), and wild squirrels' response to conspecific's alarm call was enhanced in the presence of both auditory and visual elements (Partan et al., 2009). In our study, higher level urban noise may have been masking auditory predator cues and, thus, decreasing the information received by the Eurasian

TABLE 2 Alert Distance (AD) model.

Variable	Estimate	SE	t value	Lower 95% CI	Upper 95% CI	*p*-value
Intercept	-0.03	0.08	-0.40	-0.19	0.13	0.70
SD	**0.82**	**0.04**	**19.9**	**0.74**	**0.90**	**<0.001**
Noise (dBA)	0.01	0.04	0.24	-0.08	0.10	0.81
Age (juvenile)	**0.22**	**0.10**	**2.11**	**0.02**	**0.42**	**0.04**

Results of the Generalized Linear Mixed Model (GLMM) relating AD to the predictors. The predictors include the starting Distance (SD), the individual's age (juvenile and adult), and the ambient noise level (dBA). Site (n = 11) was used as a random factor in the model. The AD is the response variable. We report estimates with the Standard Error (SE), 95% Confidence Intervals (CI), and p-values. Conditional R^2 (the proportion of variance explained by both fixed and random effects) = 0.75, and marginal R^2 (the ratio of variance explained by the fixed effects) = 0.70. Estimates with a CI not overlapping zero are considered significant and presented in bold. n = 167.

TABLE 3 Flight Initiation Distance (FID)/Alert Distance (AD) models.

Variable	Estimate	SE	t value	Lower 95% CI	Upper 95% CI	*p*-value
Intercept	-0.01	0.15	-0.10	-0.33	0.30	0.93
SD	**-0.37**	**0.07**	**-5.12**	**-0.51**	**-0.23**	**< 0.001**
Noise (dBA)	**-0.20**	**0.08**	**-2.59**	**-0.36**	**-0.04**	**0.01**
Age (juvenile)	0.08	0.18	0.45	-0.27	0.44	0.65

Results of the Generalized Linear Mixed Models (GLMM) relating FID/AD ratio to the predictors. The predictors include the starting Distance (SD), the individual's age (juvenile and adult), and the ambient noise level (dBA). Site (n = 11) was used as a random factor in the model. The ratio of FID/AD is the response variable. We report estimates with the Standard Error (SE), 95% Confidence Intervals (CI), and *p*-values. Conditional R^2 (the proportion of variance explained by both fixed and random effects) = 0.35, and marginal R^2 (the ratio of variance explained by the fixed effects) = 0.18. Estimates with a CI not overlapping zero are considered significant and presented in bold. *n* = 167.

Magpies even in the presence of normally perceived visual cues and preventing an enhanced response, which would explain the decreased FID/AD ratio at higher levels of noise while AD is unaffected. However, to confirm that combined auditory and visual predator cues cause an enhanced antipredator behavior in urban Eurasian Magpies, future experiments must follow the "multiple stimuli framework" proposed by Munoz and Blumstein (2012).

Finally, it is crucial to stress that while we made diligent efforts to control variables, the nature of our fieldwork study introduces the possibility of uncontrolled confounding variables. Consequently, the observed impact of noise on FID/AD may be influenced by other unaccounted-for variables that may have emerged during the fieldwork. We suggest future controlled settings where the researchers manipulate the noise levels to confirm better direct effects of noise on the antipredator behavior of Eurasian Magpies.

Here, we did not include human density in the models as we found a similar human activity across observations. We believe that human density was similar as we have visited the field under comparable weather conditions and times of the day. Additio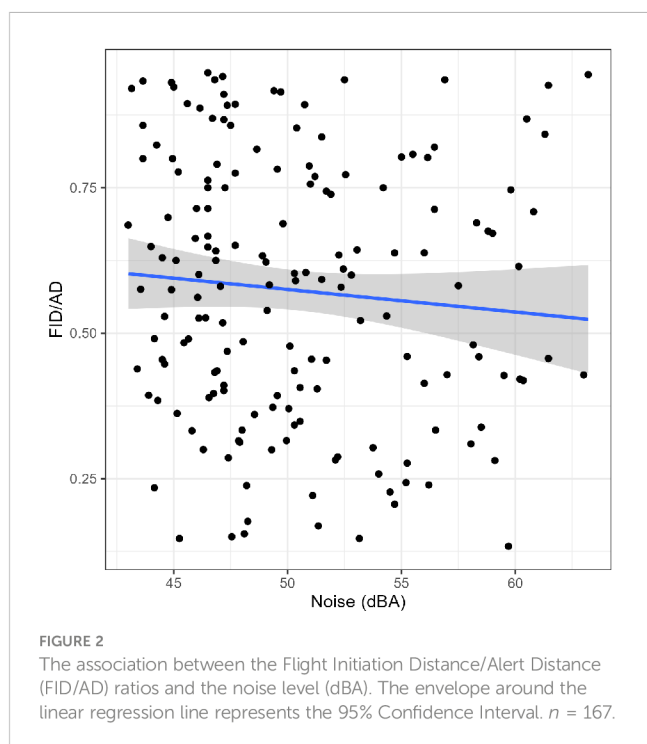nally, we believe that any slight difference in human density across different parks would be accounted for within the random factor of the park.

4.3 Antipredator behavior and age

We found that juvenile Eurasian Magpies had significantly longer ADs than adults. Their FID/AD ratios were not significantly different, meaning that younger birds detect threats earlier but take a similar time to respond. Other studies found conflicting results between juvenile and adult antipredator behavior where some found that juveniles were more vigilant (similar to our results, i.e., de Jong et al., 2021; Mohring et al., 2022), others found the opposite to be true (i.e., Koch and Paton, 2014; Kalb et al., 2019), while some found no significant differences between the two age groups (i.e., Biondi et al., 2020). In some species, behavioral plasticity allows individuals to change their behavior across their lifetime based on different selective pressures (Petelle et al., 2013). In urban areas, juveniles may still have not habituated well to the increased presence of humans and may still be wearier of people than their adult counterparts. Eurasian Magpies may increase their tolerance to people throughout their lives. In urban areas where humans are increasingly present and generally harmless, birds would benefit from reducing their fear of humans to decrease energy loss and missed opportunities due to constant fleeing (Cooper and Frederick, 2007; Díaz et al., 2021). Alternatively, adults and juveniles may have different priorities while balancing the trade-off between vigilance and other activities, especially when adults are foraging for offsprings during the breeding season, such as when the experiment was conducted.

5 Conclusions

During the breeding season, we assessed the effects of urban noise pollution on the antipredator behavior of Eurasian Magpies in Prague. We found that noise may not interfere with Eurasian Magpies' capacity to detect danger but increases their time to respond to it. We propose that the impact of noise on the escape behavior may not always reflect the same pattern in its capacity to detect the predator and suggest that future studies investigating the impact of noise on the escape behavior consider both aspects of the antipredator behavior. We also recommend future studies to compare different aspects of attention and to find the best

FIGURE 2
The association between the Flight Initiation Distance/Alert Distance (FID/AD) ratios and the noise level (dBA). The envelope around the linear regression line represents the 95% Confidence Interval. *n* = 167.

proxies of predator detection (such as using telemetric eye trackers) since birds may detect the approaching person before displaying alertness to it, and AD may not always be a very precise measure of predator detection (Yorzinski and Platt, 2014; Tätte et al., 2019).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because no Eurasian Magpies were caught or trapped. All individuals studied were present in public parks or green areas. The AD and FID of foraging Eurasian Magpies were determined by slowly approaching them until they flushed (by jumping or flying away). The experiments only cause brief and minimal disturbance to the birds and are no different than the regular background disturbance urban birds face in public parks by other visitors. Thus, the field experiments comply with the current laws of the Czechia and require no special permits.

Author contributions

FA: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. YB: Conceptualization, Methodology, Supervision, Writing – review & editing. AS: Investigation, Writing – review & editing. FM: Conceptualization, Methodology, Supervision, Writing – review & editing.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1345971/full#supplementary-material

References

Abou Zeid, F., Morelli, F., Ibáñez-Álamo, J. D., Díaz, M., Reif, J., Jokimäki, J., et al. (2023). Spatial overlap and habitat selection of corvid species in european cities. *Animals* 13, 1192. doi: 10.3390/ani13071192

Barber, J. R., Crooks, K. R., and Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol. Evol.* 25, 180–189. doi: 10.1016/j.tree.2009.08.002

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4.* R Packageversion 1. 1–4. Available at: https://cran.r-project.org/web/packages/lme4/index.html.

Benmazouz, I., Jokimäki, J., Lengyel, S., Juhász, L., Kaisanlahti-Jokimäki, M.-L., Kardos, G., et al. (2021). Corvids in urban environments: A systematic global. *Animals* 11 (11), 1–24. doi: 10.3390/ani11113226

Biondi, L. M., Fuentes, G. M., Córdoba, R. S., Bó, M. S., Cavalli, M., Paterlini, C. A., et al. (2020). Variation in boldness and novelty response between rural and urban predatory birds: The Chimango Caracara, Milvago chimango as study case. *Behav. Processes* 173, 104064. doi: 10.1016/j.beproc.2020.104064

Blumstein, D. T. (2003). Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl Manage* 67, 852–857. doi: 10.2307/3802692

Blumstein, D. T., Fernandez-Juricic, E., Ledeeà, O., Larsen, E., Rodriguez-Prieto, I., and Zugmeyer, C. (2004). Avian risk assessment: effects of perching height and detectability. *Ethology* 110, 273–285. doi: 10.1111/j.1439-0310.2004.00970.x

Blumstein, D. T., Fernández-Juricic, E., Zollner, P. A., and Garity, S. C. (2005). Inter-specific variation in avian responses to human disturbance. *J. Appl. Ecol.* 42, 943–953. doi: 10.1111/j.1365-2664.2005.01071.x

Catchpole, C. K., and Slater, P. J. B. (2003). *Bird song: biological themes and variations* (Cambridge, United Kingdom: Cambridge university press).

Chan, A. A. Y. H., David Stahlman, W., Garlick, D., Fast, C. D., Blumstein, D. T., and Blaisdell, A. P. (2010a). Increased amplitude and duration of acoustic stimuli enhance distraction. *Anim. Behav.* 80, 1075–1079. doi: 10.1016/j.anbehav.2010.09.025

Chan, A. A. Y. H., Giraldo-Perez, P., Smith, S., and Blumstein, D. T. (2010b). Anthropogenic noise affects risk assessment and attention: The distracted prey hypothesis. *Biol. Lett.* 6, 458–461. doi: 10.1098/rsbl.2009.1081

Ciebiera, O., Czechowski, P., Morelli, F., Piekarski, R., and Bocheński, M. (2021). Selection of urbanized areas by magpie pica pica in a medium size city in Poland. *Animals* 11, 1738. doi: 10.3390/ani11061738

Cooper, W. E., and Frederick, W. G. (2007). Optimal flight initiation distance. *J. Theor. Biol.* 244, 59–67. doi: 10.1016/j.jtbi.2006.07.011

Croci, S., Butet, A., and Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits? *Condor* 110, 223–240. doi: 10.1525/cond.2008.8409

de Jong, M. E., Nicolaus, M., Fokkema, R. W., and Loonen, M. J. J. E. (2021). State dependence explains individual variation in nest defence behaviour in a long-lived bird. *J. Anim. Ecol.* 90, 809–819. doi: 10.1111/1365-2656.13411

Díaz, M., Grim, T., Markó, G., Morelli, F., Alamo, J. D. I., and Jokimäki, J. (2021). Effects of climate variation on bird escape distances modulate community responses to global change. *Sci. Rep.* 1–10, 12826. doi: 10.1038/s41598-021-92273-1

Dukas, R. (2002). Behavioural and ecological consequences of limited attention. *Philos. Trans. R. Soc. B: Biol. Sci.* 357, 1539–1547. doi: 10.1098/rstb.2002.1063

Dukas, R. (2004). Causes and consequences of limited attention. *Brain Behav. Evol.* 63, 197–210. doi: 10.1159/000076781

Evans, J. C., Dall, S. R. X., and Kight, C. R. (2018). Effects of ambient noise on zebra finch vigilance and foraging efficiency. *PloS One* 13, e0209471. doi: 10.1371/journal.pone.0209471

Fernández-Juricic, E., Erichsen, J. T., and Kacelnik, A. (2004). Visual perception and social foraging in birds. *Trends Ecol. Evol.* 19, 25–31. doi: 10.1016/j.tree.2003.10.003

Fernández-Juricic, E., Jimenez, M. D., and Lucas, E. (2001). Alert distance as an alternative measure of bird tolerance to human disturbance: Implications for park design. *Environ. Conserv.* 28, 263–269. doi: 10.1017/S0376892901000273

Fernández-Juricic, E., Jimenez, M. D., and Lucas, E. (2002). Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Can. J. Zool* 80, 1212–1220. doi: 10.1139/z02-104

Fox, J., Friendly, G. G., Graves, S., Heiberger, R., Monette, G., Nilsson, H., et al. (2007). *The car package* Vol. 1109 (Vienna, Austria: R Foundation for Statistical Computing), 1431.

Francis, C. D., Ortega, C. P., and Cruz, A. (2009). Noise pollution changes avian communities and species interactions. *Curr. Biol.* 19, 1415–1419. doi: 10.1016/j.cub.2009.06.052

analysisGravolin, I., Key, M., and Lill, A. (2014). Boldness of urban Australian magpies and local traffic volume. *Avian Biol. Res.* 7, 244–250. doi: 10.3184/175815514X14151981691872

Hollén, L. I., and Radford, A. N. (2009). The development of alarm call behaviour in mammals and birds. *Anim. Behav.* 78, 791–800. doi: 10.1016/j.anbehav.2009.07.021

Hu, Y., and Cardoso, G. C. (2009). Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behav. Ecol.* 20, 1268–1273. doi: 10.1093/beheco/arp131

Kalb, N., Anger, F., and Randler, C. (2019). Flight initiation distance and escape behavior in the black redstart (*Phoenicurus ochruros*). *Ethology* 125, 430–438. doi: 10.1111/eth.12867

Karp, D. S., and Root, T. L. (2009). Sound the stressor: How Hoatzins (*Opisthocomus hoazin*) react to ecotourist conversation. *Biodivers Conserv.* 18, 3733–3742. doi: 10.1007/s10531-009-9675-6

Kern, J. M., and Radford, A. N. (2016). Anthropogenic noise disrupts use of vocal information about predation risk. *Environ. pollut.* 218, 988–995. doi: 10.1016/j.envpol.2016.08.049

Kight, C. R., and Swaddle, J. P. (2011). How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecol. Lett.* 14, 1052–1061. doi: 10.1111/ele.2011.14.issue-10

Klett-Mingo, J. I., Pavón, I., and Gil, D. (2016). Great tits, Parus major, increase vigilance time and reduce feeding during peaks of aircraft noise. *Anim. Behav.* 115, 29–34. doi: 10.1016/j.anbehav.2016.02.021

Koch, S. L., and Paton, P. W. C. (2014). Assessing anthropogenic disturbances to develop buffer zones for shorebirds using a stopover site. *J. Wildlife Manage.* 78, 58–67. doi: 10.1002/jwmg.631

Kuznetsova, A., Brockhoff, P. B., and Christensen, R. H. B. (2017). lmerTest package: tests in linear mixed effects models. *J. Stat. Softw* 82 (13), 1–26. doi: 10.18637/jss.v082.i13

Lima, S. L., and Bednekoff, P. A. (1999). Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? *Anim. Behav.* 58, 537–543. doi: 10.1006/anbe.1999.1182

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., and Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *J. Open Source Softw* 6 (60), 3139. doi: 10.21105/joss.03139

Lukas, J., Romanczuk, P., Klenz, H., Klamser, P., Arias Rodriguez, L., Krause, J., et al. (2021). Acoustic and visual stimuli combined promote stronger responses to aerial predation in fish. *Behav. Ecol.* 32, 1094–1102. doi: 10.1093/beheco/arab043

Marzluff, J. M. (2008). Island biogeography for an urbanizing world how extinction and colonization may determine biological diversity in human-dominated landscapes. In J. M. Marzluff, et al. *Urban Ecosyst.* Boston, MA: Springer. doi: 10.1007/978-0-387-73412-5_23

Meillère, A., Brischoux, F., and Angelier, F. (2015). Impact of chronic noise exposure on antipredator behavior: An experiment in breeding house sparrows. *Behav. Ecol.* 26, 569–577. doi: 10.1093/beheco/aru232

Merrall, E. S., and Evans, K. L. (2020). Anthropogenic noise reduces avian feeding efficiency and increases vigilance along an urban–rural gradient regardless of species' tolerances to urbanisation. *J. Avian Biol.* 51, 1–8. doi: 10.1111/jav.02341

Mohring, B., Angelier, F., Jaatinen, K., Steele, B., Lönnberg, E., and Öst, M. (2022). Drivers of within-and among-individual variation in risk-taking behaviour during reproduction in a long-lived bird. *Proc. R. Soc. B* 289, 20221338. doi: 10.1098/rspb.2022.1338

Møller, A. P. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol* 63, 63–75. doi: 10.1007/s00265-008-0636-y

Møller, A. P. (2021). Risk-taking behaviour as a central concept in evolutionary biology. *World at Our Fingertips*, 301–314. doi: 10.1093/oso/9780198851738.003.0017

Morelli, F., Benedetti, Y., Díaz, M., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., et al. (2019). Contagious fear: Escape behavior increases with flock size in European gregarious birds. *Ecol. Evol.* 9, 6096–6104. doi: 10.1002/ece3.5193

Morelli, F., Mikula, P., Blumstein, D. T., Díaz, M., Markó, G., Jokimäki, J., et al. (2022). Flight initiation distance and refuge in urban birds. *Sci. Total Environ.* 842, 156939. doi: 10.1016/j.scitotenv.2022.156939

Munoz, N. E., and Blumstein, D. T. (2012). Multisensory perception in uncertain environments. *Behav. Ecol.* 23, 457–462. doi: 10.1093/beheco/arr220

Partan, S. R. (2017). Multimodal shifts in noise: switching channels to communicate through rapid environmental change. *Anim. Behav.* 124, 325–337. doi: 10.1016/j.anbehav.2016.08.003

Partan, S. R., Larco, C. P., and Owens, M. J. (2009). Wild tree squirrels respond with multisensory enhancement to conspecific robot alarm behaviour. *Anim. Behav.* 77, 1127–1135. doi: 10.1016/j.anbehav.2008.12.029

Partan, S. R., and Marler, P. (2005). Issues in the classification of multimodal communication signals. *Am. Nat.* 166, 231–245. doi: 10.1086/431246

Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A., and Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Anim. Behav.* 86, 1147–1154. doi: 10.1016/j.anbehav.2013.09.016

Petrelli, A. R., Levenhagen, M. J., Wardle, R., Barber, J. R., and Francis, C. D. (2017). First to flush: The effects of ambient noise on songbird flight initiation distances and implications for human experiences with nature. *Front. Ecol. Evol.* 5. doi: 10.3389/fevo.2017.00067

Price, M. (2008). The impact of human disturbance on birds: A selective review. *Aust. Zoologist* 34, 163–196. doi: 10.7882/fs.2008.023

Quinn, J. L., Whittingham, M. J., Butler, S. J., and Cresswell, W. (2006). Noise, predation risk compensation and vigilance in the chaffinch *fringilla coelebs*. *J. Avian Biol.* 37, 601–608. doi: 10.1111/j.2006.0908-8857.03781.x

Radvan, M., Rendall, A. R., and Weston, M. A. (2023). The habitat connectivity hypothesis of escape in urban woodland birds. *Behav. Ecology* 34 (2), 297–305. doi: 10.1093/beheco/arac127

R Core Team. (2022). *R: A language and environment for statistical computing*. Available online at: https://www.R-project.org/.

Šálek, M., Grill, S., and Riegert, J. (2020). Nest-site selection of an avian urban exploiter , the Eurasian magpie *Pica pica* , across the urban-rural gradient. *J. Vertebr Biol.* 70 (1), 20086.11. doi: 10.25225/jvb.20086

Shannon, G., Crooks, K. R., Wittemyer, G., Fristrup, K. M., and Angeloni, L. M. (2016). Road noise causes earlier predator detection and flight response in a free-ranging mammal. *Behav. Ecol.* 27, 1370–1375. doi: 10.1093/beheco/arw058

Slabbekoorn, H., and Ripmeester, E. A. P. (2008). Birdsong and anthropogenic noise: Implications and applications for conservation. *Mol. Ecol.* 17, 72–83. doi: 10.1111/j.1365-294X.2007.03487.x

Sordello, R., Ratel, O., de Lachapelle, F. F., Leger, C., Dambry, A., and Vanpeene, S. (2020). Evidence of the impact of noise pollution on biodiversity: A systematic map. *Environ. Evid* 9, 1-27. doi: 10.1186/s13750-020-00202-y

Sun, J. W. C., and Narins, P. M. (2005). Anthropogenic sounds differentially affect amphibian call rate. *Biol. Conserv.* 121, 419–427. doi: 10.1016/j.biocon.2004.05.017

Tätte, K., Ibáñez-Álamo, J. D., Markó, G., Mänd, R., and Møller, A. P. (2019). Antipredator function of vigilance re-examined: vigilant birds delay escape. *Anim. Behav.* 156, 97–110. doi: 10.1016/j.anbehav.2019.08.010

Tryjanowski, P., Møller, A. P., Morelli, F., Biaduń, W., Brauze, T., Ciach, M., et al. (2016). Urbanization affects neophilia and risk-taking at bird-feeders. *Sci. Rep.* 6, 28575. doi: 10.1038/srep28575

Ware, H. E., McClure, C. J. W., Carlisle, J. D., Barber, J. R., and Daily, G. C. (2015). A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. *Proc. Natl. Acad. Sci. U.S.A.* 112, 12105–12109. doi: 10.1073/pnas.1504710112

Warren, P. S., Katti, M., Ermann, M., and Brazel, A. (2006). Urban bioacoustics: It's not just noise. *Anim. Behav.* 71, 491–502. doi: 10.1016/j.anbehav.2005.07.014

Washburn, D. A., and Taglialatela, L. A. (2006). "Attention as it is manifest across species," in *Comparative cognition: Experimental explorations of animal intelligence* (Oxford, United Kingdom: Oxford University Press), 127–142. doi: 10.1093/acprof:oso/9780195377804.003.0008

Xu, Y., Cao, Z., and Wang, B. (2020). Effect of urbanization intensity on nest-site selection by Eurasian Magpies (Pica pica). *Urban Ecosyst.* 23, 1099–1105. doi: 10.1007/s11252-020-00996-2

Yorzinski, J. L., and Platt, M. L. (2014). Selective attention in peacocks during predator detection. *Anim. Cognit.* 17, 767–777. doi: 10.1007/s10071-013-0708-x

Zhou, Y., Radford, A. N., and Magrath, R. D. (2019). Why does noise reduce response to alarm calls? Experimental assessment of masking, distraction and greater vigilance in wild birds. *Funct. Ecol.* 33, 1280–1289. doi: 10.1111/1365-2435.13333

Annex III. Flight initiation distance and refuge in urban birds.

Federico Morelli*, Peter Mikula, Daniel T. Blumstein, Mario Díaz, Gábor Markó, Jukka Jokimäki, Marja-Liisa Kaisanlahti-Jokimäki, Kristina Floigl, **Farah Abou Zeid**, Anastasiia Siretckaia, Yanina Benedetti, 2022.

Author contributions:

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Flight initiation distance and refuge in urban birds

Federico Morelli [a,*], Peter Mikula [b], Daniel T. Blumstein [c], Mario Díaz [d], Gábor Markó [e],
Jukka Jokimäki [f], Marja-Liisa Kaisanlahti-Jokimäki [f], Kristina Floigl [a], Farah Abou Zeid [a],
Anastasiia Siretckaia [a], Yanina Benedetti [a]

[a] Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Kamýcká 129, CZ-165 00 Prague 6, Czech Republic
[b] Institute of Vertebrate Biology, Czech Academy of Sciences, Květná 8, 603 65 Brno, Czech Republic
[c] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA
[d] Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (BGC-MNCN-CSIC), E-28006 Madrid, Spain
[e] Department of Plant Pathology, Institute of Plant Protection, Hungarian University of Agriculture and Life Sciences, Ménesi út 44, Budapest 1118, Hungary
[f] Nature Inventory and EIA-services, Arctic Centre, University of Lapland, P. O. Box 122, FI-96101 Rovaniemi, Finland

HIGHLIGHTS

- Flight initiation distance (FID) is considered a proxy of antipredator behaviour.
- We investigated changes in FID of birds in relation to refuge type and availability.
- We found that birds preferred tree refuges over artificial and bush refuges.
- Birds escaped earlier if the distance to the nearest available refuge was longer.
- Birds fled longer distances to the refuge when were more afraid (with longer FID).

GRAPHICAL ABSTRACT
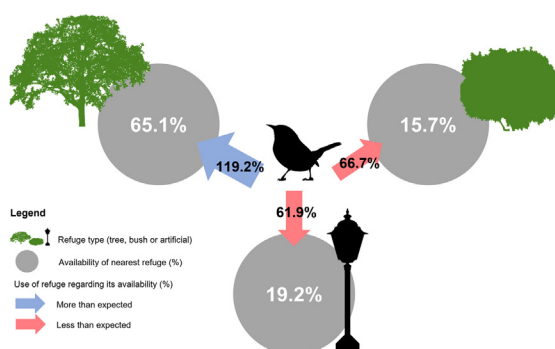
ABSTRACT

Risk-taking in birds is often measured as the flight initiation distance (FID), the distance at which individuals take flight when approached by a potential predator (typically a human). The ecological factors that affect avian FID have received great attention over the past decades and meta-analyses and comparative analyses have shown that FID is correlated with body mass, flock size, starting distance of the approaching human, density of potential predators, as well as varying along rural to urban gradients. However, surprisingly, only few studies (mainly on reptiles and mammals) have explored effects of different types of refugia and their availability on animal escape decisions.

We used Bayesian regression models (controlling for the phylogenetic relatedness of bird species) to explore changes in escape behaviour recorded in European cities in relationship to the birds' distance to the nearest refuge and distance fled to the refuge. In our analyses, we also included information on the type of refuge, built-up and vegetation cover, starting distance, flock size, urbanization level, and type of urban habitat. We found that birds preferred tree refuges over artificial and bush refuges. Birds escaped earlier if the distance to the nearest refuge of any type was longer and if birds fled longer distances to the refuge. FID was shorter when birds used bushes as refugia or landed on the ground after flushing compared to using artificial refugia. Similarly, the distance fled to a refuge was shortest when using bushes, and increased when escaping to artificial substrates and trees. Birds were more timid in suburban than core areas of cities, cemeteries than parks, and in areas with higher bush cover but lower cover of built-up

* Corresponding author.
  E-mail address: fmorellius@gmail.com (F. Morelli).

areas and trees. Our findings provide novel information regarding the importance of refuge proximity and type as factors affecting the escape behaviour of urban birds.

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1. Introduction

There are three different defensive mechanisms that can be adopted for a prey when facing a predatory threat: avoiding detection through camouflage, evading the capture by escaping and trying to deter the predator (Kalb et al., 2019). However, the most common action for a prey confronting a predatory threat is to escape (Lima and Dill, 1990). An early escape can reduce foraging efficiency or increase physiological costs, while, on the other hand, a delayed escape can increase the risk of mortality due to predation (Ydenberg and Dill, 1986). In birds, fearfulness and willingness to take a risk is frequently estimated as the flight initiation distance (FID) when an individual bird is approached by a human under standardized conditions. Across species, FID is typically positively correlated with body size, perhaps because larger species which live longer and delay their reproduction minimize mortality due to predation by taking fewer risks (Virkkala and Lehikoinen, 2014; Wasser and Sherman, 2010), and they take a longer time to get airborne and thus avoid capture (Fernández-Juricic et al., 2006; Hemmingsen, 1951; Møller, 2008a; Weston et al., 2012). Finally, the number of birds in a flock can positively affect FID, probably due to "many eyes" scanning and increased vigilance (Morelli et al., 2019; Pulliam, 1973). The flock size seems to be more related to FID than to the distance moved during the escape (Tätte et al., 2018).

Among the environmental factors affecting FID, many studies have focused on the characteristics of habitat related to a degree of urbanization (Samia et al., 2017), interactions between predators and prey (Møller, 2008b), predator abundance (Díaz et al., 2022, 2013), level of stress of individuals (Tablado et al., 2021), as well as the time of day and season when FID is measured (Mikula et al., 2018; Piratelli et al., 2015). FID could be modulated by food abundance, being shorter in areas with lower food availability (Møller et al., 2015). Variation in the weather also can affect the escape behaviour, with FIDs expected to decrease with increasing temperature and precipitation (Díaz et al., 2021). Additionally, some researchers suggested that birds are able to adapt their escape behaviour strategies to specific characteristics of human-modified habitats, including a road's speed limit (Legagneux and Ducatez, 2013) or the type and intensity of human activities (Morelli et al., 2018).

Shelter is a key factor regulating many aspects of predator–prey interactions (Berryman and Hawkins, 2006). Although FID is well-studied in relation to several ecological factors, and despite that the type and distance to refuge is predicted to affect escape responses (Cooper and Frederick, 2007; Ydenberg and Dill, 1986), the empirical effects of refuge characteristics are still poorly known and understood. Most of the studies on the effects of refuge characteristics on escape behaviour focused on mammals (Bonenfant and Kramer, 1996; Dill and Houtman, 1989) and reptiles (Martín and López, 2003; Zani et al., 2009), with only sporadic reports on birds (e.g. Blumstein et al., 2004; Hall et al., 2020; Møller, 2012). Although objects used by birds as refuges, including trees, bushes or artificial structures, are important components of the landscape occupied, no systematic research was conducted to quantify the main effects of refuge characteristics on FID in European birds. This is important, since behavioral responses of animals to human disturbance can have important implications for conservation and management (Weston et al., 2012). In the wildlife tourism sector as well as in urban areas, wildlife managers can use FID in sensitivity and tolerance analyses, which permit them to identify areas beyond which animals are less disturbed by humans (Fernández-Juricic et al., 2005; Livezey et al., 2016; Samia et al., 2015).

We expect that birds approached by predators and/or humans select among available refuges based on the characteristics of the surrounding environment, and the distance and type of available refuge. Thus, we hypothesized that birds escape earlier when the available refuge is far (i.e. FID will be positively associated with potential refuge distance), since a short distance to a potential refuge should decrease the real or perceived risk of predation (Dill and Houtman, 1989; Stankowich and Blumstein, 2005). This is because we expect that when birds are farther away from a potential refuge, the time to reach that refuge is longer, therefore their risk of being captured is higher. Additionally, considering that FID is a measure of fearfulness, we can also expect that birds escaping early (longer FID) will fly longer distances to the used refuge (Tätte et al., 2018). A previous study showed a positive association between FID and distance fled after the escape, mainly for larger birds, suggesting that the distance fled is also an informative measure of antipredator behaviour in birds (Tätte et al., 2018). Escape distances of birds may also be affected by vegetation structure and decrease with increasing cover of trees and bushes which are often used as refuges by birds (Fernández-Juricic et al., 2002). Some refuge types may be perceived as safer than other types of refuges (Lima, 1993) and are related to predator avoidance strategies.

The aim of this study is to compare the escape distances (measured as FID) of birds in relation to distance to the potential refuge, distance fled to the refuge, refuge type and its availability in urban areas in four European countries. First, we explored how the availability of different types of refuges affect frequency of their use by birds and whether the distance fled to the refuge differed between the different types of refuges. We then employed multi-predictor Bayesian phylogenetically informed regression models controlling for the effects of several potentially important factors such as starting distance, flock size, levels of urbanization or habitat type.

2. Methods

2.1. Study area, flight initiation distance and refuge type

Data on the flight initiation distance (FID) of birds were collected in urban areas in five cities in four European countries (Table S1) during the breeding seasons of 2020 and 2021. The data were mainly collected during the first 4 h after sunrise (6:00–10:00) on weekdays when it was not raining or excessively windy (Beaufort number ≤ 2). Observers used binoculars to identify birds that were foraging or engaged in "relaxed behaviour" (i.e. roosting or preening). Each individual bird was approached in a straight line by the observer walking at a slow, constant speed. The starting distance was estimated as the distance between the observer and the target when the observer started the approach toward the target (Blumstein, 2013). FID was measured as the distance between the observer and the point where the bird started to escape (fleeing or running). We collected data from as many bird species as possible by systematic searches of the study areas, but avoided sampling the same individual twice by moving to another site immediately after a bird was sampled. Highly vigilant birds (individuals clearly nervous, or altered by the presence of humans before the start of the approach), or birds sitting on their nests were avoided.

Flock size was defined as the number of conspecifics moving or foraging together; individuals in the flock were close to each other and were visually separated from individuals that were not occurring in the same flock. No mixed-species flocks were approached in this study.

Each sampled site was classified regarding the level of urbanization into two categories: core (central, densely inhabited and well-urbanized parts of the city) and suburban (areas peripherical to the city centre); the main type of habitat: cemetery, garden, other urban areas (streets, any other urban type of green area) or park. The surrounding area around the FID sampling points was described in terms of land use, considering a fixed radius of 50 m around the observer. We estimated the land use cover in terms of percentage of built-up areas, trees, bushes, and grass. We used the following definition of bush and tree: A bush is a multi-stemmed short woody plant

branching at or near the ground, while a tree is a tall perennial plant with a single self-supporting woody stem (Götmark et al., 2016). Additionally, in our study, trees were often taller than bushes (> 4 m).

From the point where the target bird was observed, we estimated the distance to the nearest available refuge, considering the following types: artificial (e.g. electric wire, fence, statue, monument, signal pole, etc.), bush, or tree or patch of trees. We also calculated the mean distance to the nearest available refuge of each type.

After flushing the bird and measuring FID, we recorded the type of refuge used by the bird (artificial, bush, or tree) and the distance fled to such refuge from the point of escape. If the bird flew away without using a refuge (e.g. it landed on the ground) or was impossible to identify it, the fields "type of refuge" and "distance to refuge" were not filled.

2.2. Statistical analyses

First, a preliminary exploration of the data was performed by using all of the data, without considering any phylogenetic relationships between bird species. A Pearson's chi-square test of independence was performed to examine the relationship between availability of the nearest and the selected refuge, among all types of refuges (i.e. artificial, bush, or tree). For this test, if the bird flew and then landed on the ground, this was not considered as a refuge (approx. 30 % of total observations). The distance fled to the used refuge was compared among the different types of refuges using a Games-Howell paired test (Triola, 2012).

Second, we considered the non-independence in data values regarding the bird species. We used only species with ≥10 observations, because such sampling provides reliable estimates of FID (Sol et al., 2018). During the data selection procedure, we excluded all observations for mallards (*Anas platyrhynchos*) and other waterbirds as we wanted to focus on terrestrial birds. We tested associations between FID (response variable) and a set of predictors and covariates by multi-predictor Bayesian phylogenetically informed regression models, using the 'brms' v. 2.6.13 package (Bürkner,

2017). In the first model, we modelled FID as a function of mean distance of the nearest available refuge of each type, starting distance, flock size, land use composition (built-up cover, bush cover, grass cover, tree cover), level of urbanization (core, suburban) and habitat type (cemetery, garden, other urban areas, park). The category grass cover was excluded from the modelling procedure to avoid multicollinearity issues, since it was strongly negatively correlated with built-up cover ($r = -0.64$, $p < 0.05$).

In the second model, we modelled FID as a function of the distance fled to the refuge, type of used refuge (artificial, bush, tree; birds which landed on ground were also included in the analyses to control for their effect), starting distance, flock size, land use composition, level of urbanization, and habitat type.

To control for statistical non-independence due to shared ancestry among species (Paradis, 2011), we included species as a random factor and a phylogenetic covariance matrix in the models. We randomly downloaded 100 species-level phylogenies (using the "Hackett backbone") from BirdTree web tool (http://birdtree.org) (Jetz et al., 2012). We then constructed the maximum credibility tree (using these 100 trees) using maxCladeCred function in the 'phangorn' v. 2.8.1 package (Schliep, 2011) and created a phylogenetic covariance matrix using inverseA function in the 'MCMCglmm' v. 2.32 package (Hadfield, 2010). We controlled for spatial variation by including country as a random factor in the models. We excluded all observations with missing information on all predictors (for sample sizes in each test, see figures and tables). We also fitted models that used species as a random factor but did not incorporate the phylogenetic covariance matrix; we compared both types of models using the widely applicable information criterion (WAIC) and the leave-one-out information criterion (LOOIC) using the 'loo' package (Vehtari et al., 2017) and found that both model types provided qualitatively almost identical results but phylogenetically informed models were slightly better (although differences in WAIC and LOOIC values were <2 in all cases). Hence, we report only results of the phylogenetically informed models in the main text (for results of non-phylogenetic models, see Table S3-4).
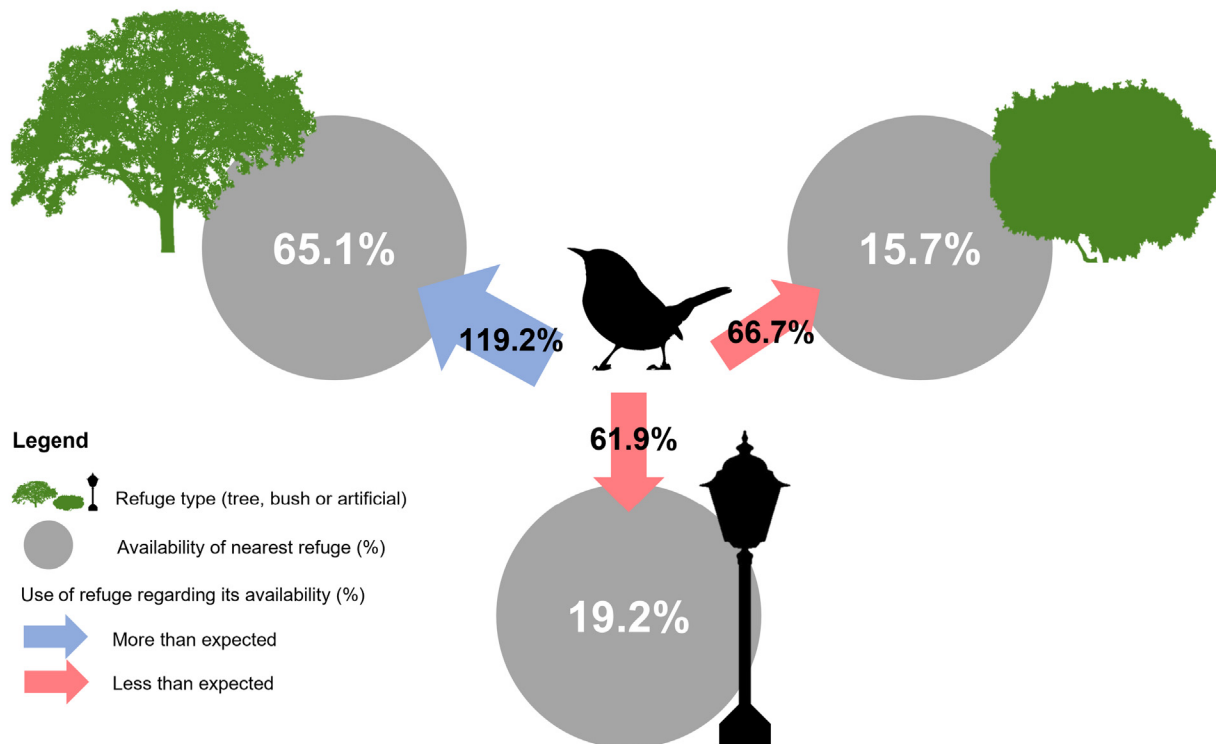
Fig. 1. Schematic representation of the mean availability of the nearest refuge of each type and mean effective use of each type of refuge by birds in urban habitats. Availability and use are showed in percentage. The sum of availability of nearest refuges reaches the 100 %. The percentage of use of each type of refuge is calculated as the rate between effective use regarding the total availability of such type of nearest refuge, so values are unlinked among different types of refuge. The colour and thin of arrows indicate if the type of refuge is used more (light blue) or less (light red) than expected regarding its availability. $N = 1506$.
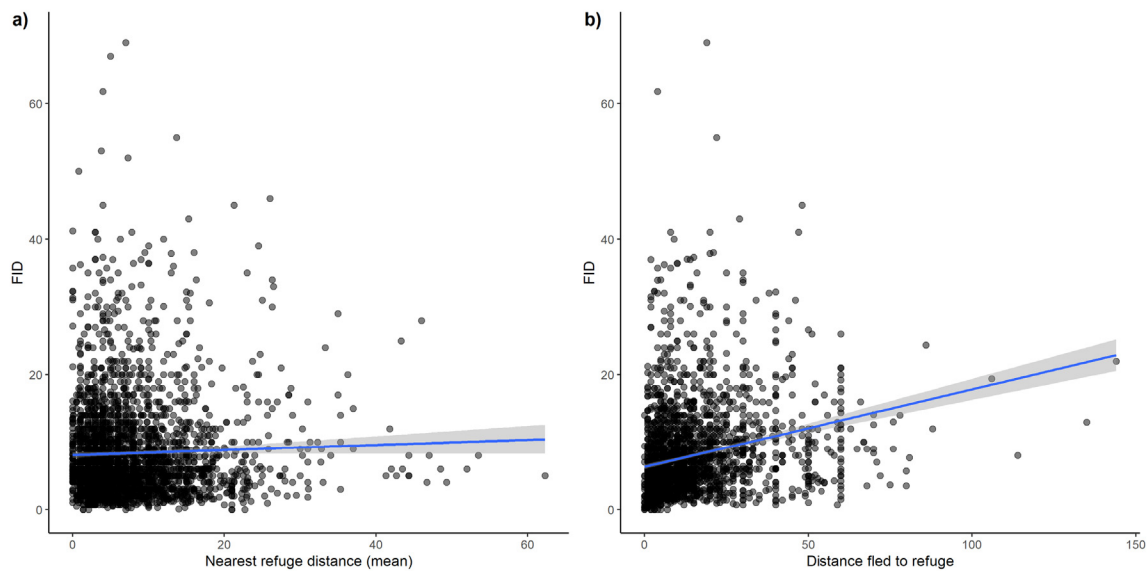
Fig. 2. Association between flight initiation distance (FID, m) and (a) mean nearest available refuge distance (m) and (b) distance fled to the used refuge (m), for birds sampled in this study. Envelopes around linear regression lines are 95 % confidence intervals. $N = 2816$ (mean nearest available refuge distance) and $N = 2458$ (distance fled to the used refuge).

Models were fitted using a Gaussian family and a log-link function. For each model, we ran four Markov Chain Monte Carlo chains with default priors (i.e. uninformative, flat priors for fixed effects) and used 4000 sampling iterations (2000 iterations as a warm-up period). To minimize the occurrence of divergent transitions, we increased the target average proposal acceptance probability to 0.999 and the maximum tree depth to 15 (Bürkner, 2017). Model diagnostics indicated a good model convergence with an R of 1 or close to 1 and sufficient effective sample size in the bulk and in the tails of the distribution (Vehtari et al., 2021). All continuous predictors were centred and scaled. For each model, we calculated the conditional R^2 (the proportion of variance explained by fixed and random effects) and marginal R^2 (the proportion of variance explained by the fixed effects only) using r2_bayes function in the 'performance' v. 0.8.0 package (Lüdecke et al., 2021). All statistical analyses and data explorations were performed with R software v. 4.1.2 (R Development Core Team, 2021).

3. Results

A total of 2900 FID observations were collected for 85 bird species recorded in four European countries (Table S1). The most frequently observed bird species were *Columba palumbus*, *Passer domesticus*, *Columba livia*, *Pica pica*, *Turdus merula* and *Parus major*, accounting for >59.2 % of the total observations (Table S2). Overall, bird species with the longest FID were *Sturnus unicolor* and *Picus viridis* (mean FID >17 m, $N = 51$ and 25 observations, respectively). The two species with shortest FID were *Columba livia* and *Corvus corone* (mean FID = 4 and 4.2 m, $N = 312$ and 37 observations, respectively). Considering all species together, the mean values of FID across the five European cities ranged from 4.1 m (standard deviation = 2.7 m) (Budapest, Hungary) to 11.6 m (standard deviation = 8.8 m) (Toledo, Spain) (Table S1).

The most common nearest type of refuge available in all sampling sites was tree and tree patches (981 cases), followed by artificial structures (289 cases) and bush (237 cases) (Fig. 1). The mean distances to the nearest refuge available varied from 4.9 m (± 4.4 m standard deviation) (Toledo, Spain) to 13.5 m (± 10.7 m) (Rovaniemi, Finland) (Table S1). Considering the relative availability of each type of refuge, trees were overused as refuge while bush and artificial structures were underused ($X^2 = 58.09$, df = 2, $p < 0.001$; Fig. 1).

Birds escaped earlier (i.e. had a longer FID) when the mean distance to nearest refuge of each type and starting distance were longer (Fig. 2;

Table 1). Birds escaped earlier in suburban than in core areas of the cities, in areas with higher bush cover and lower built-up and tree cover, and in cemeteries than in parks (Fig. 3; Table 1).

The results of the second model identified a marginally significant effect that birds escaped earlier when they were farther from the used refuge (Fig. 2; Table 2). FID differed between birds using different types of refuges: FID was shorter when birds escaped to bushes or landed on the ground compared to escaping to an artificial refuge (Fig. 2; Table 2). Avian FID also increased with starting distance and bush cover and were longer in suburban than core city areas. Conversely, FID decreased with increasing built-up

Table 1

Results of a multi-predictor Bayesian phylogenetically informed regression model exploring the associations between flight initiation distance (response variable) and a set of predictors: mean distance to the nearest refuge of each type, starting distance, flock size, land use composition (built-up cover, bush cover, tree cover), level of urbanization (core, suburban) and habitat type (cemetery, garden, other urban areas, park). The model incorporated a species (and a phylogenetic covariance matrix) and country as random factors to control for statistical phylogenetic and spatial non-independence in data values. We report parameter estimates with their standard errors (SE) and 95 % credible intervals, conditional R^2 (the proportion of variance explained by fixed and random effects) and marginal R^2 (the proportion of variance explained by the fixed effects only). Significant results (i.e., those where credible intervals do not cross zero) are highlighted in bold. $N = 2309$ observations and 34 species.

Variables	Estimate	SE	Lower 95 % CI	Upper 95 % CI
Fixed factors				
Intercept	2.06	0.38	1.30	2.83
Distance to nearest refuge	**0.07**	**0.01**	**0.05**	**0.10**
Starting distance	**0.19**	**0.01**	**0.17**	**0.21**
Flock	−0.01	0.01	−0.04	0.01
Built-up cover	**−0.09**	**0.02**	**−0.13**	**−0.06**
Bush cover	**0.06**	**0.02**	**0.02**	**0.09**
Tree cover	**−0.05**	**0.02**	**−0.09**	**−0.01**
Urban level (Suburban)	**0.25**	**0.03**	**0.20**	**0.30**
Habitat (Garden)	−0.15	0.10	−0.35	0.03
Habitat (Other urban)	0.04	0.07	−0.09	0.18
Habitat (Park)	**−0.25**	**0.05**	**−0.35**	**−0.14**
Random factors				
Country	0.60	0.44	0.20	1.79
Species	0.44	0.07	0.33	0.60
Conditional R^2	0.40		0.37	0.42
Marginal R^2	0.12		0.01	0.31
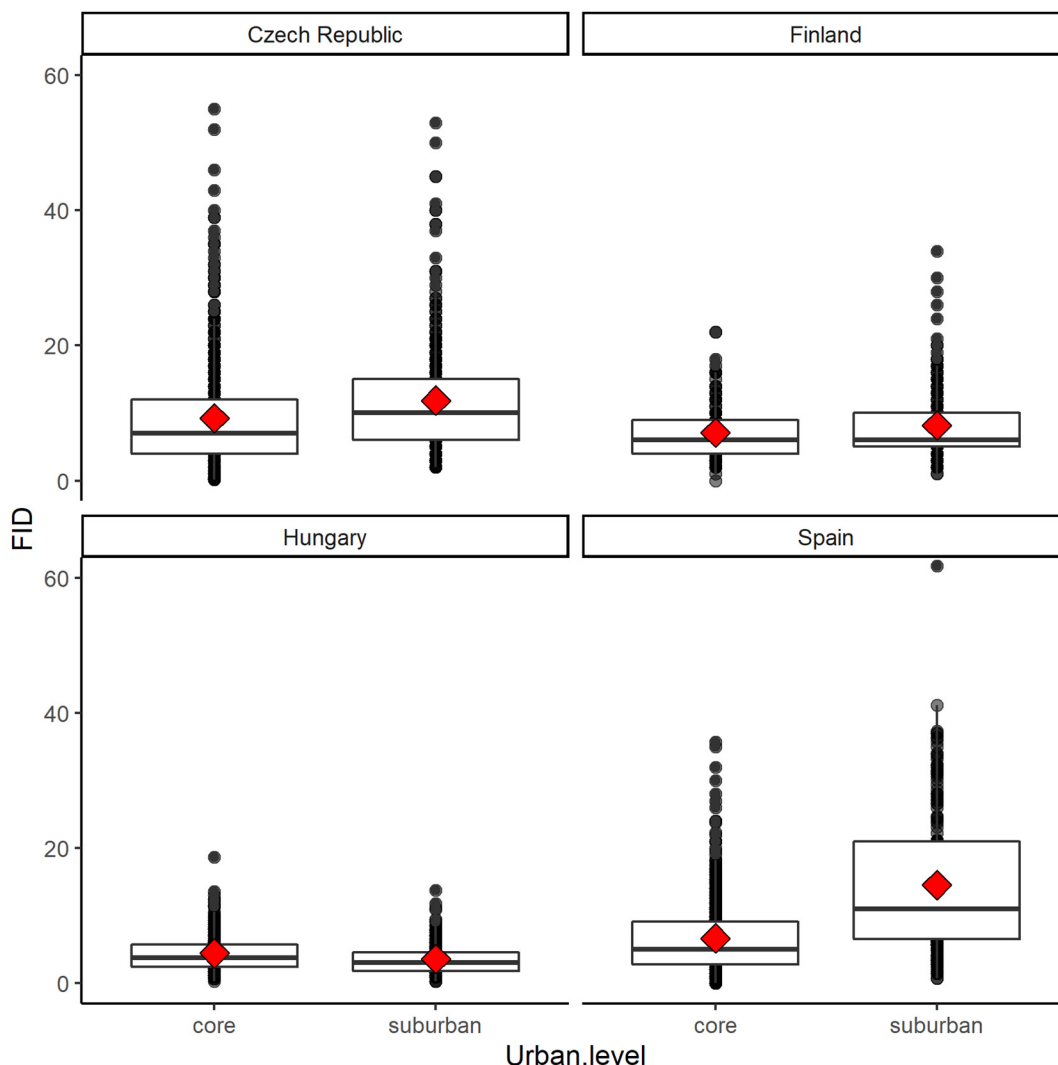
Fig. 3. Association between flight initiation distance (FID, m) of birds and level of urbanization (core or suburban) in the four countries sampled in this study (Czech Republic, Finland, Hungary and Spain). Box plots show the median (the bar in the middle of rectangles), upper and lower quartiles (length of rectangles), maximum and minimum values (whiskers), mean values (red rhombus), and raw FID values (small gray dots). N total = 2878 (Czech Republic, core = 701, suburban = 354; Finland, core = 158, suburban = 208; Hungary, core = 207, suburban = 175; Spain, core = 688, suburban = 387).

habitat and tree cover and was shorter in parks than in cemeteries (Table 2). Finally, we found that birds flew longer distances to an artificial or tree refuge than when they aimed for a bush refuge (Games-Howell paired test, p < 0.001 for comparison bush vs. artificial, p < 0.001 for comparison bush vs. tree, Fig. S1).

4. Discussion

We found that risk perception in birds and their escape decisions were affected by distance to the refuge and type of refuge used, as well as by the built up area and vegetation cover. We found that birds escaped earlier when the potential or used refugia were farther (illustrating how distance to safety influenced risk assessment), and in areas with high bush cover but low built-up and tree cover (illustrating that for the species studied, this type of cover was obstructive rather than protective). Birds also fled farther when they used artificial and trees as refuges, rather than bushes, or when they landed on the ground. Finally, we also found that FID of birds included in this study was related to some of well-studied factors such as starting distance and the level of urbanization. Hence, our results suggest that several environmental factors related to the availability and characteristics of refuges affect avian antipredator behaviour and their decision when and where to escape.

The main findings of this study are related to the birds' escape response in relation to the distance to the available and used refuge. We found that birds escaped earlier if: (a) the potential refuge was farther away, and (b) birds had to fly longer distances to the refuge. This final statement was only marginally significant in the modelling procedure, but the positive association was more clear when exploring FID on bird species with larger samples (Fig. S2). Similar findings have been reported for diverse animals, including fishes, reptiles, and mammals. For common wall lizards (*Podarcis muralis*) the distance to the nearest refuge alters escape behaviour (Amo et al., 2005). Similarly to our findings, gray squirrels (*Sciurus carolinensis*) (Dill and Houtman, 1989), woodchucks (*Marmota monax*) (Bonenfant and Kramer, 1996), Cuban curly-tailed lizards (*Leiocephalus carinatus*) (Cooper, 2007), broad-headed skinks (*Eumeces laticeps*) (Cooper, 1997), and African cichlid fishes (*Melanochromis chipokae*) (Dill, 1990) escaped earlier as distance to refuge increased. In contrast to Tätte et al. (2018), we found that FID of birds generally increases with the distance to the nearest available refuge in urban green areas, supporting a prediction of optimal escape theory (Cooper and Frederick, 2007; Ydenberg and Dill, 1986). This implies that birds base their escape decisions also on the relative time required to reach the refuge. Thus, birds could be more afraid of a predatory threat when farther away from a potential refuge.

Table 2
Results of a multi-predictor Bayesian phylogenetically informed regression model exploring the associations between flight initiation distance (response variable) and a set of predictors: distance fled to refuge, type of used refuge (artificial, bush, tree; ground category – even if was not classified as a type of refuge – was also included), starting distance, flock size, land use composition (built-up cover, bush cover, tree cover), level of urbanization (core, suburban) and habitat type (cemetery, garden, other urban areas, park). The model incorporated species (and a phylogenetic covariance matrix) and country as random factors to control for statistical phylogenetic and spatial non-independence in data values. We report parameter estimates with their standard errors (SE) and 95 % credible intervals, conditional R^2 (the proportion of variance explained by fixed and random effects) and marginal R^2 (the proportion of variance explained by the fixed effects only). Significant and marginally significant results (i.e., those where credible intervals do not cross zero or slightly cross zero, respectively) are highlighted in bold and italics, respectively. N = 1953 observations and 33 species.

Variables	Estimate	SE	lower 95 % CI	upper 95 % CI
Fixed factors				
Intercept	2.11	0.34	1.44	2.77
Distance fled to refuge	0.02	0.01	−0.00	0.04
Refuge type (Bush)	**−0.66**	**0.12**	**−0.91**	**−0.43**
Refuge type (Ground)	**−0.26**	**0.06**	**−0.37**	**−0.15**
Refuge type (Tree)	−0.05	0.05	−0.14	0.04
Starting distance	**0.21**	**0.01**	**0.19**	**0.23**
Flock	−0.02	0.02	−0.06	0.01
Built-up cover	**−0.11**	**0.02**	**−0.16**	**−0.07**
Bush cover	**0.06**	**0.02**	**0.03**	**0.10**
Tree cover	**−0.05**	**0.02**	**−0.08**	**−0.01**
Urban level (Suburban)	**0.22**	**0.03**	**0.16**	**0.28**
Habitat (Garden)	−0.11	0.10	−0.31	0.08
Habitat (Other urban)	0.06	0.07	−0.09	0.20
Habitat (Park)	**−0.18**	**0.06**	**−0.29**	**−0.06**
Random factors				
Country	0.51	0.37	0.17	1.53
Species	0.38	0.07	0.28	0.53
Conditional R^2	0.43		0.40	0.45
Marginal R^2	0.19		0.02	0.39

Additionally, we found that longer FIDs were associated with longer distances fled to the refuge, independently of the type of refuge selected. A relationship between FID and distance fled to the refuge is relatively poorly understood, and has been mostly studied in lizards (Cooper, 2007; Cooper and Wilson, 2007). A previous study in birds already found a positive association between FID and fleeing distance, but only in heavier species (Tätte et al., 2018). Our study covering tens of bird species, found a similar pattern suggesting pre- and post-disturbance symmetry in their fear; birds with longer FIDs are also birds that escaped farther. This result supports the hypothesis that individual level of fearfulness is a personality trait and, hence, is consistent among different phases of a predatory encounter (Cooper and Wilson, 2007; Stankowich and Coss, 2007); shyer individuals have longer FIDs and fled longer distances than bolder individuals. Yet, studies of yellow-bellied marmots (*Marmota flaviventer*) suggest that boldness may be age-specific (Petelle et al., 2013). Future avian studies would benefit from testing identified individuals (Blumstein, 2019) and it would be interesting to identify animal groups which adopt different escape strategies.

We also found that FID and distances fled were influenced by the availability of various types of refugia, with earlier escapes and longer distances fled when using artificial structures and trees as refugia than bush or landing on the ground. The earlier escape and longer distance fled to trees (despite their prevalence) may be explained by preferences (Fig. 1). The generally low distance fled to bush refuge may indicate that birds often feed in the proximity of this type of refuge. Some previous studies found no relationship between escape distances of birds and vegetation structure and type of area cover (Rodriguez-Prieto et al., 2009), but we provide evidence that vegetation and built-up cover may affect escape decision (Fernández-Juricic et al., 2002; Morelli et al., 2018). These findings may further support the observation that birds in our sample tended to prefer trees as refuges and were willing to flee longer distances to trees. Artificial

structures (e.g. street lamps or buildings), although not used as frequently as trees, may be perceived by birds as safer refuges because they are typically higher than bushes and, hence, birds might respond to approaching humans by decreasing their escape distances in built-up areas with prevalent artificial structures and be willing to flee farther when using an artificial refuge. In the visited urban parks and cemeteries, the cover of green areas identified as a potential refuge (bush and trees) was not particularly higher in suburban areas than in core city areas (Fig. S3). More work on how birds perceive the built environment is necessary to develop wildlife-friendly cities (Uchida et al., 2021).

Our results also confirmed some findings previously demonstrated in birds. We found a positive and significant association between FID and starting distance which has been widely identified birds, including European urban populations (Blumstein, 2013; Mikula et al., 2021; Tätte et al., 2018). In addition, we found that, overall, FID of birds was longer in suburban areas if compared with core areas of the city, with the only exception of Budapest (Hungary) (see Fig. 3). This result is congruent with numerous previous studies showing a significant effect of the urbanization gradient on avian escape behaviour, with consistently longer avian FID in rural than urban habitats (Møller et al., 2015; Samia et al., 2017, 2015) or FID decreasing with the proximity to the city centre (Battle et al., 2016; Matsyura et al., 2015). Birds from suburban areas could be more sensitive to approaching humans than their conspecifics from the core city areas, because they are less tolerant of anthropogenic disturbances (Bötsch et al., 2018; Samia et al., 2015; Tryjanowski et al., 2020). Interestingly, we found that birds in cemeteries were shier (escaped earlier) than birds in parks. This is in contrast with previous European study which sampled FID of birds during breeding season 2014 in Czech Republic, France, Italy and Poland and found the opposite pattern (Morelli et al., 2018). This may indicate that differences in avian FID between parks and cemeteries may be temporally variable and differ between various countries (Morelli et al., 2018).

In conclusion, the present study found that escape decision of birds and their willingness to take a risk is affected by their distance to the potential refuge, the availability of different refuge types as well as vegetation and built-up cover. Environmental characteristics related to the potential refuge distribution and availability have been neglected in studies on escape behaviour of animals, and birds in particular. This study indicates that avian escape behaviour takes into account refuge proximity and type as well as the general structure of the surrounding environment. Future studies could explore how the availability of refuges and their types interact with spatial and temporal heterogeneity in humans and predator activity and affect avian antipredator behaviour.

CRediT authorship contribution statement

FM, PM, MD, GM, JJ, M-L K–J, KF, FAZ, AS, YB collected data; FM and YB suggested hypotheses; FM and PM designed and performed the statistical analysis; FM, PM, DTB and YB wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data availability statement

Data will be made available after the publication, under reasonable request to the authors.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.156939.

References

Amo, L., López, P., Martín, J., 2005. Flexibility in antipredatory behavior allows wall lizards to cope with multiple types of predators. Ann. Zool. Fennici 42, 109–121.

Battle, K.E., Foltz, S.L., Moore, I.T., 2016. Predictors of flight behavior in rural and urban songbirds. Wilson J. Ornithol. 128, 510–519. https://doi.org/10.1676/1559-4491-128.3.510.

Berryman, A.A., Hawkins, B.A., 2006. The refuge as an integrating concept in ecology and evolution. Oikos 115, 192–196. https://doi.org/10.1111/j.0030-1299.2006.15188.x.

Blumstein, D.T., 2003. Flight-initiation distance in birds is dependent on intruder starting distance. J. Wildl. Manag. 67, 852–857.

Blumstein, D.T., 2019. What chasing birds can teach us about predation risk effects: past insights and future directions. J. Ornithol. 160, 587–592. https://doi.org/10.1007/s10336-019-01634-1.

Blumstein, D.T., Fernández-Juricic, E., LeDee, O., Larsen, E., Rodriguez-Prieto, I., Zugmeyer, C., 2004. Avian risk assessment: effects of perching height and detectability. Ethology 110, 273–285. https://doi.org/10.1111/j.1439-0310.2004.00970.x.

Bonenfant, M., Kramer, D.L., 1996. The influence of distance to burrow on flight initiation distance in the woodchuck, Marmota monax. Behav. Ecol. 7, 299–303. https://doi.org/10.1093/beheco/7.3.299.

Bötsch, Y., Gugelmann, S., Tablado, Z., Jenni, L., 2018. Effect of human recreation on bird anti-predatory response. PeerJ 6, e5093. https://doi.org/10.7717/peerj.5093.

Bürkner, P.C., 2017. "brms": an R package for Bayesian multilevel models using Stan. J. Stat. Softw. 80, 1–28.

Cooper, J., 1997. Escape by a refuging prey, the broad-headed skink (Eumeces laticeps). Can. J. Zool. 75, 943–947. https://doi.org/10.1139/z97-113.

Cooper, W.E., 2007. Escape and its relationship to pursuit-deterrent signalling in the Cuban curly-tailed lizard Leiocephalus carinatus. Herpetologica 63, 144–150. https://doi.org/10.1655/0018-0831(2007)63[144:EAIRTP]2.0.CO;2.

Cooper, W.E., Frederick, W.G., 2007. Optimal time to emerge from refuge. Biol. J. Linn. Soc. 91, 375–382. https://doi.org/10.1111/j.1095-8312.2007.00802.x.

Cooper, W.E., Wilson, D.S., 2007. Beyond optimal escape theory: microhabitats as well as predation risk affect escape and refuge use by the phrynosomatid lizard Sceloporus virgatus. Behaviour 144, 1235–1254. https://doi.org/10.1163/156853907781890940.

Díaz, M., Møller, A.P., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., Markó, G., Tryjanowski, P., 2013. The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. PLoS One 8, e64634. https://doi.org/10.1371/journal.pone.0064634.

Díaz, M., Grim, T., Markó, G., Morelli, F., Ibáñez Alamo, J.D., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Tätte, K., Tryjanowski, P., Møller, A.P., 2021. Effects of climate variation on bird escape distances modulate community responses to global change. Sci. Rep. 11, 12826. https://doi.org/10.1038/s41598-021-92273-1.

Díaz, M., Fernández, J., Page, A., 2022. Cat colonies and flight initiation distances of urban birds: dealing with conflicting sources of citizen wellbeing. Sci. Total Environ. 827, 154401. https://doi.org/10.1016/j.scitotenv.2022.154401.

Dill, L.M., 1990. Distance-to-cover and the escape decisions of an African cichlid fish, Melanochromis chipokae. Environ. Biol. Fishes 27, 147–152. https://doi.org/10.1007/BF00001944.

Dill, L.M., Houtman, R., 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (Sciurus carolinensis). Can. J. Zool. 67, 233–235. https://doi.org/10.1139/z89-033.

Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2002. Factors affecting intra- and interspecific variations in the difference between alert distances and flight distances for birds in forested habitats. Can. J. Zool. 80, 1212–1220.

Fernández-Juricic, E., Venier, M.P., Renison, D., Blumstein, D.T., 2005. Sensitivity of wildlife to spatial patterns of recreationist behavior: a critical assessment of minimum approaching distances and buffer areas for grassland birds. Biol. Conserv. 125, 225–235. https://doi.org/10.1016/j.biocon.2005.03.020.

Fernández-Juricic, E., Blumstein, D.T., Abrica, G., Manriquez, L., Adams, L.B., Adams, R., Daneshrad, M., Rodriguez-Prieto, I., 2006. Relationships of anti-predator escape and post-escape responses with body mass and morphology: a comparative avian study. Evol. Ecol. Res. 8, 731–752.

Götmark, F., Götmark, E., Jensen, A.M., 2016. Why be a shrub? A basic model and hypotheses for the adaptive values of a common growth form. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.01095.

Hadfield, J.D., 2010. MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. J. Stat. Softw. 33, 1–22.

Hall, M.J., Burns, A.L., Martin, J.M., Hochuli, D.F., 2020. Flight initiation distance changes across landscapes and habitats in a successful urban coloniser. Urban Ecosyst. https://doi.org/10.1007/s11252-020-00969-5.

Hemmingsen, A., 1951. The relation of shyness (flushing distance) to body size. Spolia Zool. Musei Hauniensis 11, 74–76.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. Nature 491, 444–448. https://doi.org/10.1038/nature11631.

Kalb, N., Anger, F., Randler, C., 2019. Flight initiation distance and escape behavior in the black redstart (Phoenicurus ochruros). Ethology 125, 430–438. https://doi.org/10.1111/eth.12867.

Legagneux, P., Ducatez, S., 2013. European birds adjust their flight initiation distance to road speed limits. Biol. Lett. 9, 20130417.

Lima, S.L., 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. Wilson Bull. 105, 1–47.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640. https://doi.org/10.1139/z90-092.

Livezey, K.B., Fernández-Juricic, E., Blumstein, D.T., 2016. Database of bird flight initiation distances to assist in estimating effects from human disturbance and delineating buffer areas. J. Fish Wildl. Manag. 7, 181–191. https://doi.org/10.3996/082015-JFWM-078.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. No titleperformance: an R package for assessment, comparison and testing of statistical models. J. Open Source Softw. 6, 3139.

Martín, J., López, P., 2003. Changes in the escape responses of the lizard Acanthodactylus erythrurus under persistent predatory attacks. Copeia 408–413. https://doi.org/10.1643/0045-8511(2003)003[0408:CITERO]2.0.CO;2.

Matsyura, A., Jankowski, K., Zimaroeva, A., 2015. Escape behaviours of Corvidae in an urban ecosystem of Zhytomyr (Ukraine). Rom. J. Biol. 60, 125–134.

Mikula, P., Díaz, M., Albrecht, T., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Kroitero, G., Møller, A.P., Tryjanowski, P., Yosef, R., Hromada, M., 2018. Adjusting risk-taking to the annual cycle of long-distance migratory birds. Sci. Rep. 8, 13989. https://doi.org/10.1038/s41598-018-32252-1.

Mikula, P., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Markó, G., Morelli, F., Møller, A.P., Szakony, S., Yosef, R., Albrecht, T., Tryjanowski, P., 2021. Face mask-wear did not affect large-scale patterns in escape and alertness of urban and rural birds during the COVID-19 pandemic. Sci. Total Environ. 793, 148672. https://doi.org/10.1016/j.scitotenv.2021.148672.

Møller, A.P., 2008a. Flight distance of urban birds, predation and selection for urban life. Behav. Ecol. Sociobiol. 63, 63–75. https://doi.org/10.1007/s00265-008-0636-y.

Møller, A.P., 2008b. Interactions between interactions: predator-prey, parasite-host, and mutualistic interactions. Ann. N. Y. Acad. Sci. 1133, 180–186. https://doi.org/10.1196/annals.1438.007.

Møller, A.P., 2012. Urban areas as refuges from predators and flight distance of prey. Behav. Ecol. 23, 1030–1035. https://doi.org/10.1093/beheco/ars067.

Møller, A.P., Tryjanowski, P., Díaz, M., Kwieciński, Z., Indykiewicz, P., Mitrus, C., Goławski, A., Polakowski, M., 2015. Urban habitats and feeders both contribute to flight initiation distance reduction in birds. Behav. Ecol. 26, 861–865. https://doi.org/10.1093/beheco/arv024.

Morelli, F., Mikula, P., Benedetti, Y., Bussière, R., Jerzak, L., Tryjanowski, P., 2018. Escape behaviour of birds in urban parks and cemeteries across Europe: evidence of behavioural adaptation to human activity. Sci. Total Environ. 631–632, 803–810. https://doi.org/10.1016/j.scitotenv.2018.03.118.

Morelli, F., Benedetti, Y., Díaz, M., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Tätte, K., Markó, G., Jiang, Y., Tryjanowski, P., Møller, A.P., 2019. Contagious fear: escape behavior increases with flock size in European gregarious birds. Ecol. Evol. 9, 6096–6104. https://doi.org/10.1002/ece3.5193.

Paradis, E., 2011. Analysis of Phylogenetics And Evolution With R.

Petelle, M.B., McCoy, D.E., Alejandro, V., Martin, J.G.A., Blumstein, D.T., 2013. Development of boldness and docility in yellow-bellied marmots. Anim. Behav. 86, 1147–1154. https://doi.org/10.1016/j.anbehav.2013.09.016.

Piratelli, A.J., Favoretto, G.R., de Almeida Maximiano, M.F., 2015. Factors affecting escape distance in birds. Zoologia 32, 438–444. https://doi.org/10.1590/S1984-46702015000600002.

Pulliam, H., 1973. On the advantages of flocking. J. Theor. Biol. 38, 419–422.

R Development Core Team, 2021. R: A Language And Environment for Statistical Computing.

Rodriguez-Prieto, I., Fernández-Juricic, E., Martín, J., Regis, Y., 2009. Antipredator behavior in blackbirds: habituation complements risk allocation. Behav. Ecol. 20, 371–377. https://doi.org/10.1093/beheco/arn151.

Samia, D.S.M., Nakagawa, S., Nomura, F., Rangel, T.F., Blumstein, D.T., 2015. Increased tolerance to humans among disturbed wildlife. Nat. Commun. 6, 8877. https://doi.org/10.1038/ncomms9877.

Samia, D.S.M., Blumstein, D.T., Diaz, M., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., Tätte, K., Marko, G., Tryjanowski, P., Møller, A.P., 2017. Rural-urban differences in escape behavior of European birds across a latitudinal gradient. Front. Ecol. Evol. 5, 66. https://doi.org/10.3389/fevo.2017.00066.

Schliep, K.P., 2011. phangorn: phylogenetic analysis in R. Bioinformatics 27, 592–593.

Sol, D., Maspons, J., Gonzalez-Voyer, A., Morales-Castilla, I., Garamszegi, L.Z., Møller, A.P., 2018. Risk-taking behavior, urbanization and the pace of life in birds. Behav. Ecol. Sociobiol. 72, 59. https://doi.org/10.1007/s00265-018-2463-0.

Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. Proc. R. Soc. B Biol. Sci. 272, 2627–2634. https://doi.org/10.1098/rspb.2005.3251.

Stankowich, T., Coss, R.G., 2007. Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. Behav. Ecol. 18, 358–367. https://doi.org/10.1093/beheco/arl086.

Tablado, Z., Bötsch, Y., Bókony, V., Angelier, F., Lendvai, Á.Z., Jenni-Eiermann, S., Jenni, L., 2021. Factors modulating the behavioral and physiological stress responses: do they modify the relationship between flight initiation distance and corticosterone reactivity? Horm. Behav. 132, 104979. https://doi.org/10.1016/j.yhbeh.2021.104979.

Tätte, K., Møller, A.P., Mänd, R., 2018. Towards an integrated view of escape decisions in birds: relation between flight initiation distance and distance fled. Anim. Behav. 136, 75–86. https://doi.org/10.1016/j.anbehav.2017.12.008.

Triola, M.F., 2012. Elementary Statistics. 12th ed. Pearson International, London, UK.

Tryjanowski, P., Kosicki, J.Z., Hromada, M., Mikula, P., 2020. The emergence of tolerance of human disturbance in neotropical birds. J. Trop. Ecol. 36, 1–5. https://doi.org/10.1017/S0266467419000282.

Uchida, K., Blakey, R.V., Burger, J.R., Cooper, D.S., Niesner, C.A., Blumstein, D.T., 2021. Urban biodiversity and the importance of scale. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2020.10.011.

Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. 27, 1413–1432. https://doi.org/10.1007/s11222-016-9696-4.

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., Bürkner, P.-C., 2021. Rank-normalization, folding, and localization: an improved R̂ for assessing convergence of MCMC. Bayesian Anal. 16, 667–718.

Virkkala, R., Lehikoinen, A., 2014. Patterns of climate-induced density shifts of species: poleward shifts faster in northern boreal birds than in southern birds. Glob. Chang. Biol. 20, 2995–3003. https://doi.org/10.1111/gcb.12573.

Wasser, D.E., Sherman, P.W., 2010. Avian longevities and their interpretation under evolutionary theories of senescence. J. Zool. https://doi.org/10.1111/j.1469-7998.2009.00671.x.

Weston, M.A., Mcleod, E.M., Blumstein, D.T., Guay, P.J., 2012. A review of flight-initiation distances and their application to managing disturbance to Australian birds. Emu 112, 269–286. https://doi.org/10.1071/MU12026.

Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. Adv. Study Behav. 16, 229–249. https://doi.org/10.1016/S0065-3454(08)60192-8.

Zani, P.A., Jones, T.D., Neuhaus, R.A., Milgrom, J.E., 2009. Effect of refuge distance on escape behavior of side-blotched lizards (Uta stansburiana). Can. J. Zool. 87, 407–414. https://doi.org/10.1139/Z09-029.

Annex IV. EVI and NDVI as proxies for multifaceted avian diversity in urban areas.

Yanina Benedetti*, Corey T. Callaghan, Iva Ulbrichová, Antonia Galanaki, Theodoros Kominos, **Farah Abou Zeid**, Juan Diego Ibáñez-Álamo, Jukka Suhonen, Mario Díaz, Gábor Markó, Raphaël Bussière, Piotr Tryjanowski, Nikos Bukas, Marko Mägi, Lucas Leveau, Fabio Pruscini, Leszek Jerzak, Olaf Ciebiera, Jukka Jokimäki, Marja-Liisa Kaisanlahti-Jokimäki, Anders Pape Møller, Federico Morelli, 2023.

Author contributions:

Conceptualization and methodology, Y.B. and F.M.; data collection: C.T.C., A.G., T.K., J.D.I.A., J.S., M.D., G.M., R.B., P.T., N.B., M.M., F.P., L.J., O.C., J.J., M.L.K.J., A.P.M., and F.M.; data analyses: Y.B. and F.M., **writing – original draft**, Y.B., C.T.C., **F.A.Z.**, and I.U.; **writing – review & editing**: Y.B., C.T.C., I.U., A.G., T.K., **F.A.Z**, J.D.I.A., J.S., M.D., G.M., R.B., P.T., N.B., M.M., L.L., F.P., L.J., O.C., J.J., M.L.K.J., A.P.M., and F.M.

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EVI and NDVI as proxies for multifaceted avian diversity in urban areas

Yanina Benedetti[1] | Corey T. Callaghan[2,3,4] | Iva Ulbrichová[5] |
Antonia Galanaki[6] | Theodoros Kominos[6] | Farah Abou Zeid[1] |
Juan Diego Ibáñez-Álamo[7] | Jukka Suhonen[8] | Mario Díaz[9] | Gábor Markó[10] |
Raphaël Bussière[11] | Piotr Tryjanowski[12] | Nikos Bukas[13] | Marko Mägi[14] |
Lucas Leveau[15] | Fabio Pruscini[16] | Leszek Jerzak[17] | Olaf Ciebiera[17] |
Jukka Jokimäki[18] | Marja-Liisa Kaisanlahti-Jokimäki[18] | Anders Pape Møller[19] |
Federico Morelli[1]

[1]Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

[2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[3]Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, UNSW Sydney, Sydney, New South Wales, Australia

[4]Department of Wildlife Ecology and Conservation, Fort Lauderdale Research and Education Center, University of Florida, Davie, Florida, USA

[5]Faculty of Forestry and Wood Sciences, Department of Forest Ecology, Czech University of Life Sciences Prague, Prague, Czech Republic

[6]Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece

[7]Department of Zoology, Faculty of Sciences, University of Granada, Granada, Spain

[8]Department of Biology, University of Turku, Turku, Finland

[9]Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (BGC-MNCN-CSIC), Madrid, Spain

[10]Department of Plant Pathology, Institute of Plant Protection, Hungarian University of Agriculture and Life Sciences, Budapest, Hungary

[11]Liniers, France

[12]Institute of Zoology, Poznań University of Life Sciences, Poznań, Poland

[13]Plegadis, Ioannina, Greece

[14]Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

[15]Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires–IEGEBA (CONICET–UBA), Ciudad Universitaria, Buenos Aires, Argentina

[16]Urbino, Italy

[17]Institute of Biological Sciences, University of Zielona Góra, Zielona Góra, Poland

[18]Nature Inventory and EIA-services, Arctic Centre, University of Lapland, Rovaniemi, Finland

[19]Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, Orsay Cedex, France

Correspondence
Yanina Benedetti
Email: ybenedetti73@gmail.com

Abstract

Most ecological studies use remote sensing to analyze broad-scale biodiversity patterns, focusing mainly on taxonomic diversity in natural landscapes. One of the most important effects of high levels of urbanization is species loss (i.e., biotic homogenization). Therefore, cost-effective and more efficient methods to monitor biological communities' distribution are essential. This study explores whether the Enhanced Vegetation Index (EVI) and the Normalized Difference

Vegetation Index (NDVI) can predict multifaceted avian diversity, urban tolerance, and specialization in urban landscapes. We sampled bird communities among 15 European cities and extracted Landsat 30-meter resolution EVI and NDVI values of the pixels within a 50-m buffer of bird sample points using Google Earth Engine (32-day Landsat 8 Collection Tier 1). Mixed models were used to find the best associations of EVI and NDVI, predicting multiple avian diversity facets: Taxonomic diversity, functional diversity, phylogenetic diversity, specialization levels, and urban tolerance. A total of 113 bird species across 15 cities from 10 different European countries were detected. EVI mean was the best predictor for foraging substrate specialization. NDVI mean was the best predictor for most avian diversity facets: taxonomic diversity, functional richness and evenness, phylogenetic diversity, phylogenetic species variability, community evolutionary distinctiveness, urban tolerance, diet foraging behavior, and habitat richness specialists. Finally, EVI and NDVI standard deviation were not the best predictors for any avian diversity facets studied. Our findings expand previous knowledge about EVI and NDVI as surrogates of avian diversity at a continental scale. Considering the European Commission's proposal for a Nature Restoration Law calling for expanding green urban space areas by 2050, we propose NDVI as a proxy of multiple facets of avian diversity to efficiently monitor bird community responses to land use changes in the cities.

KEYWORDS
avian specialization, biodiversity, bird, enhanced vegetation index, normalized difference vegetation index, remote sensing, urban tolerance, VIIRS night-time lights

INTRODUCTION

Worldwide urbanization is rising, and approximately 60% of the world's population is expected to live in cities by 2030 (United Nations, 2017). Urbanization is a significant threat to biodiversity, modifying biotic and abiotic ecosystem characteristics (Grimm et al., 2008) through fragmentation or replacing natural habitats (Sklenicka, 2016; Williams et al., 2009). At the same time, urbanization generates new habitats suitable for a few species capable of adapting to novel urban environments (McKinney, 2002, 2006). Unsurprisingly then, taxonomic (Marzluff, 2001), functional (Devictor et al., 2007), and phylogenetic (Ibáñez-Álamo et al., 2016; Morelli et al., 2016; Sol et al., 2014) diversity decreased in urban environments compared with their rural or natural counterparts. More specifically, along an urbanization gradient, species richness generally decreases (e.g., Melles et al., 2003). However, it may peak at intermediate levels of urbanization (Batáry et al., 2018; Blair, 1996; Jokimäki & Suhonen, 1993; Leveau & Leveau, 2005). Although even some urban areas show increased taxonomic diversity (Blair, 1996), it usually consists of the replacement of local native species, also called "urban avoiders" (Blair, 1996), by increasingly spreading non-natives (Devictor et al., 2008; McKinney, 2002, 2006), and the predominance of generalist species, generally more tolerant to high urbanized areas (Devictor et al., 2008). Consequently, urbanization leads to biotic homogenization (McKinney, 2002, 2006).

Bird assemblages are affected by local resources and how they use suitable habitats (Croci et al., 2008). Therefore, local environmental factors better explain bird species richness (BSR) and composition than regional and landscape factors, suggesting that site-specific management strategies can improve avian diversity in cities (Croci et al., 2008; Evans et al., 2009). Managing green areas within cities could increase avian diversity (Croci et al., 2008). For example, there are a greater number of native bird species, less urban-tolerant species, in those areas composed predominantly of native vegetation (Blair, 1996). Conversely, few species, principally non-native ones, more urban tolerant, dominate areas at higher built-up land cover levels (Blair, 1996). At intermediate levels of urbanization, avian assemblages can be composed of native and non-native species. Therefore, an important first step in urban development planning is understanding factors influencing avian diversity (Stagoll et al., 2012). Moreover, to successfully carry out land management plans, it is

necessary to quantify the relationship between avian diversity and habitat features (Mcfarland et al., 2012).

The decline of biodiversity affects species richness and functional richness, increasing taxonomic and functional biotic homogenization (Ibarra et al., 2015). Indeed, the biotic homogenization process substitutes specialists with generalist species, both spatially and temporally (McKinney, 2006; Sol et al., 2014). Specialist species occupy narrower niches. For example, they exploit particular habitats and limited portions of available resources (Clavel et al., 2011). In contrast, generalist species use a wider range of habitats and greater diversity of available resources (Ducatez et al., 2015; Irschick et al., 2005). Thus, species responses to habitat loss would depend on the degree of specialization (Webb, 2010), favoring those with wider niche breadths to survive in more degraded habitats and increasing the risk of extinction of those with a high degree of specialization (Davies et al., 2004; McKinney & Lockwood, 1999). Recently, Callaghan, Benedetti, et al. (2020) highlighted a negative association between avian species specialization and their urban tolerance. Thus, considering that biodiversity involves many facets (Carmona et al., 2012), conservation ecologists claimed to apply a more integrative approach to estimate biodiversity by disentangling different facets of species assemblages (Carmona et al., 2012; Zupan et al., 2014), mainly in urbanized landscapes (Devictor et al., 2007; Morelli, Benedetti, Ibáñez-Álamo, et al., 2021). The different responses of taxonomic diversity, functional diversity, and phylogenetic diversity to environmental gradients lead to different patterns in their spatial distribution (Bässler et al., 2016; Devictor et al., 2010; Tucker & Cadotte, 2013). For these reasons, conserving different facets of biodiversity, such as taxonomic, functional, and phylogenetic diversity, including also, specialization and urban tolerance assessments, are relevant for a comprehensive understanding of biodiversity drivers (Dehling et al., 2014; Grass et al., 2015), and applying more effective conservation strategies (Brooks et al., 2006; Lee & Jetz, 2008).

Monitoring species distribution using traditional field surveys is challenging and logistically expensive. Thus, standardized evaluations of the environmental conditions with an adequate spatial resolution (Seto et al., 2004). In addition, species distribution surveys in large areas are challenging for ecologists and fieldworkers since they require high sampling effort (Palmer, 1995). Therefore, developing new methods of assessing species diversity using environmental variables could easily provide more insights into the anthropogenic and natural disturbances affecting biodiversity (Rocchini et al., 2010, 2016). In recent years, the constant availability of multispectral remote-sensed imagery has led to the widespread use of imagery with a growing resolution and quality (Huang et al., 2021).

The quality of images is adequate for the evaluation of various vegetation aspects such as canopy phenology, seasonal changes in the leaf area, and gross primary production (Liu et al., 2011; Muraoka et al., 2013; Turner et al., 2005), as well as the floristic composition, vegetation height, and structure, vitality and age (Lausch et al., 2016). So, the use of remote sensing tools largely improved the ability to monitor biodiversity and ecosystem functioning at large scales providing useful information on the species distribution, reproductive fitness (Regos et al., 2021), and population abundance (Arenas-Castro et al., 2019) when facing spatial and temporal changes (Lausch et al., 2016). Among many vegetation indices, Normalized Difference Vegetation Index (NDVI hereafter) and Landsat-derived Enhanced Vegetation Index (EVI hereafter) are the most commonly used to obtain vegetation information (Huete, Didan, Miura, & Rodriguez, 2002; Mildrexler et al., 2009; Peckham et al., 2008). Many studies demonstrated the capacity of EVI and NDVI global-based vegetation indices to track vegetation characteristics and changes at different spatial scales (Dobson et al., 2015; Gonsamo, 2010; Nieto et al., 2015; Turner et al., 2001) and across long time series (Dutrieux et al., 2015; Pettorelli et al., 2005; Semeraro et al., 2019). Both vegetation indices share many spectral-domain attributes. For this reason, they are complementary in identifying vegetation changes and canopy biophysical parameters (Huete & Justice, 1999; Semeraro et al., 2019). EVI and NDVI values are calculated based on the visible red and near-infrared spectral reflectance (top-of-atmosphere—TOA or surface reflectance). Specifically, the NDVI value calculation uses the visible red and near-infrared spectral reflectance from all land surface types, including vegetated surfaces (Huete & Justice, 1999). The index varies between −1 and 1, indicating different vegetation levels from vegetation-free cover up to high vegetation biomass (Pettorelli, 2013; Tucker, 1979). Several studies showed that NDVI value is positively related to the biomass of vegetation (Matsushita et al., 2007), vegetation structure (Caruso et al., 2017), as well as, the amount of leaf chlorophyll (Lausch et al., 2016), and leaf area coverage (Wang et al., 2005). NDVI is one of the most used global-based vegetation index. NDVI is characterized by removing the noise produced by ever-changing sun angles, topography, clouds or shadow, and atmospheric conditions (Huete, 1988; Zhengxing et al., 2003). EVI is an "optimized" vegetation index from NDVI developed to reduce some atmospheric conditions and canopy background noise and is more receptive to canopy structural variations, including leaf area index (LAI), canopy type, plant physiognomy, and canopy architecture (Huete, Didan, Miura, & Rodriguez, 2002; Huete & Justice, 1999). Similarly to NDVI, EVI values calculation uses spectral reflectance, either TOA or surface, in the visible red and near-infrared spectra. However, unlike NDVI, EVI uses the blue band for the atmospheric

correction and constant soil factor (Liu & Huete, 2019). For these reasons, EVI is demonstrated to be more reliable in low and high vegetation cover and adjusts to soil influence, canopy background signals, and atmospheric effects on vegetation index values (Gao et al., 2000; Liu & Huete, 2019). Thus, many researchers have preferred the EVI index in their studies (e.g., Boles et al., 2004; Nagler et al., 2005; Soudani et al., 2006; Waring et al., 2006). However, both vegetation indices have different constraints and do not provide direct measures of the vegetation attributes but act as proxies (Son et al., 2014). Other studies focusing on NDVI and EVI comparisons showed contrasting results in their capacities to obtain information on the vegetation attributes (Son et al., 2014). One commonly recognized obstacle with NDVI is its lower sensitivity at high vegetation biomass (Huete, 1988; Zhengxing et al., 2003) and the effects of atmospheric and background soil reflectance (Huang et al., 2021; Huete & Justice, 1999). Conversely, EVI surpasses these constraints, increasing the detection accuracy in regions at high biomass (Semeraro et al., 2019). However, EVI is more affected by the topography, becoming a challenge in hilly terrains (Matsushita et al., 2007).

NDVI and EVI are the most common vegetation indices used in ornithological studies (Bae et al., 2018; Bonthoux et al., 2018; Cooper et al., 2020; Hobi et al., 2017; Leveau et al., 2020; Pettorelli et al., 2011; Wu et al., 2013). Both vegetation indices have been documented as excellent proxies for primary productivity (e.g., Box et al., 1989; Cramer et al., 1999) and the spatiotemporal distribution of vegetation (Pettorelli et al., 2005). Because primary productivity influences the diversity and distribution of species (Wright, 1983), EVI and NDVI were identified as good predictors of avian diversity in several studies. Specifically, several authors found a positive relationship between EVI and NDVI with avian species richness in both natural (Bae et al., 2018; Cooper et al., 2020; Hobi et al., 2017; Hurlbert & Haskell, 2003; Mcfarland et al., 2012; St-Louis et al., 2009) and urban areas (Bino et al., 2008; Callaghan, Major, et al., 2020; Leveau, 2019; Leveau et al., 2018, 2020). Some studies on urban areas found contrasting associations between NDVI and avian diversity (Bae et al., 2018; Leveau et al., 2020). For example, Bae et al., 2018, found a positive association between NDVI and species richness, displaying a concave curve. While for functional and phylogenetic diversity, the association was negative and characterized by a convex curve. These results (Hawkins, Porter, & Diniz-Filho, 2003) demonstrated that the productivity–diversity correlation has not had a universal form (Hawkins, Porter, & Diniz-Filho, 2003). In addition, most of the urban studies were mainly conducted in single or few urbanized localities (e.g., cities, towns) (Argentina: Leveau et al., 2018, 2020; Leveau, 2019; Brazil: Souza et al., 2019; Jerusalem: Bino et al., 2008; Taiwan: Lin et al., 2008), potentially

limiting the transferability of such results to different cities at a national or continental scale. Therefore, more studies on a larger geographical scale (e.g., Callaghan, Major, et al., 2020) are needed to discover EVI or NDVI potential in tracking multifaceted avian diversity changes in urban areas.

The spectral heterogeneity hypothesis argued for a positive correlation between habitat heterogeneity and species diversity (Palmer et al., 2002; Rocchini et al., 2010). It was demonstrated in several taxa, for example, vascular plants (Foody & Cutler, 2006; Gould, 2000; Levin et al., 2007), lichens (Waser et al., 2004), ants (Lassau et al., 2005), birds (Bino et al., 2008; St-Louis et al., 2009), and mammals (Oindo & Skidmore, 2002). Accordingly, many studies demonstrated a positive association between the spatial heterogeneity of vegetation (assessed by EVI and NDVI spatial standard deviation) with species richness (Bacaro et al., 2011; Bergen et al., 2007; Coops et al., 2009; Culbert et al., 2012; Price et al., 2013) by monitoring and quantifying significant vegetation characteristics (e.g., change of broadleaf vegetation LAI or the phenological heterogeneity of vegetation layers) (Davi et al., 2006; Qiao et al., 2019). However, many mechanisms can change these associations when focusing on different facets of avian diversity or habitats (e.g., urban areas). Consequently, more studies are essential to understand better the associations between surrogates of habitat heterogeneity (as EVI or NDVI standard deviations) with each facet of avian diversity in cities.

Since each diversity component discloses different attributes of avian communities, more efficient monitoring across large regions in a short period should be essential to support urban avian diversity. Accordingly, more specific vegetation indices as proxies for each facet of avian diversity metrics can help to indicate potential vulnerabilities of avian communities facing climatic and land uses changes. Therefore, in this study, we investigated and compared the capacity of EVI and NDVI (as most common proxies of primary productivity and vegetation heterogeneity proxies) to determine the best-fitted surrogate of every single facet composing avian diversity (e.g., taxonomic, functional, and phylogenetic diversity, urban tolerance, and avian specialization) in 15 different European cities. We hypothesized that increasing primary productivity and vegetation heterogeneity should increase levels of avian taxonomic, functional, and phylogenetic diversity according to the (1) productivity-diversity relationship (Wright, 1983) and (2) habitat-heterogeneity hypothesis (MacArthur & MacArthur, 1961). Regarding avian specialization, we hypothesized that increasing the cover of vegetation biomass (primary productivity) and vegetation heterogeneity could be associated with a higher number of avian species that are less urban tolerant and more specialized.

METHODS

Bird data collection

Data on bird presence and abundance were collected during the breeding season along a continent-wide latitudinal gradient in 15 European cities (Figure 1; Appendix S1: Table S1). The bird survey period was performed between early April and late July 2018. The field surveys started by considering the differences in the study areas' seasons to mitigate potential issues associated with avian detectability (e.g., early April in southern Spain and the end or late May

FIGURE 1 Location of the 15 different European cities used in this study: Prague (Czech Republic); Tartu (Estonia); Jyväskylä (Finland); Turku (Finland); Poitiers (France); Athens and Ioannina (Greece); Budapest (Hungary); Pesaro (Italy); Groningen (Netherlands); Poznań and Zielona Góra (Poland); Granada, Madrid, and Toledo (Spain). See detailed results in Benedetti & Morelli (2022).

in northern Finland) (Kéry et al., 2005). Local expert ornithologists performed avian surveys to reduce potential bias due to different skills.

One observer (the same local expert ornithologists for each city) surveyed the avian composition early morning (from 6:00 to 10:00) only during good weather conditions (no rain and heavy winds). Approximately one hundred 5-min single-visit point counts (hereafter referred to as "sample site") per city distributed evenly along an urbanization gradient. All birds, visually or acoustically identified to the species level, were recorded. More specifically, the sample sites consisted of a fixed area with a 50-m radius. Sample sites were located in urbanized areas and were recorded with a GPS in decimal degrees (DD). According to GPS technical specifications from the manufacturer (Garmin), the horizontal GPS accuracy was within $\pm$5–10 m, and the vertical accuracy was within $\pm$15–38 m under normal conditions. All sample sites were distanced by at least 200 m, a standardized method in ecology (Bibby et al., 1992). This survey was designed to obtain data about the distribution and abundance of diurnal songbirds (Bibby et al., 1992). Additionally, we excluded the raptors, nocturnal species, and aerial feeders (i.e., swallows and swifts) from the analysis because the sample site method is inappropriate for estimating their abundance.

EVI and NDVI estimation

We calculated the EVI and NDVI. EVI is an extension of NDVI, which approximates vegetation and canopy structure with improved sensitivity in high biomass regions (Huete, Didan, Miura, Rodriguez, Gao, & Ferreira, 2002; Jiang et al., 2008). The EVI and NDVI values fluctuate from -1 to 1, where positive values correspond to the cover of vegetated areas, while negative ones are for water bodies, snow, clouds, and non-vegetated surfaces (Holben, 1986; Vermote, 2013). To calculate EVI and NDVI, we used Google Earth Engine (Gorelick et al., 2017) to conduct our analysis, using the USGS Landsat 8 Collection 1 Tier 1 imagery (see details in the Google Earth Engine catalog here: https://developers.google.com/earth-engine/datasets/catalog/LANDSAT_LC08_C02_T1_RT_TOA). Landsat 8 provides 30-m resolution data, with a temporal resolution of one image in ~16 days. Therefore, 2 or 3 images per month were obtained for each sample site (i.e., bird survey). To overcome the potentially limited number of images for a given sample site, we used scenes from 2017, 2018, and 2019 (expanding 1 year to either side of the bird surveys), averaging any potential interannual variation in vegetation changes. This expanded time scale was also necessary as we filtered for cloud cover on a

per-pixel basis, meaning that if only 1 year was used, some pixels could potentially have no imagery for a given month. We filtered the data using the BQA bit 4, filtering out pixels associated with cloud cover—this is a quality assessment variable provided by the USGS, associated with the Landsat 8 imagery. We also removed pixels with low cloud shadow confidence. After this filtering, we collapsed the remaining scenes for each pixel by taking the median EVI and NDVI at each pixel, minimizing the potential of outliers in the imagery. For each sampling site (i.e., bird survey), we calculated the mean and standard deviation value of the pixels within a 50-m buffer (corresponding to the bird survey 50-m sample site) separately for April, May, June, and July (corresponding to the bird survey period). We tested this robustness by calculating the mean and standard deviation of the pixels with a 150-m buffer but found that the values were strongly correlated with the 50-m buffer values (Appendix S1: Figure S1).

Finally, using monthly EVI and NDVI values (considering April to July period to match the bird survey period), we calculated the average (EVI mean and NDVI mean) and standard deviation (EVI sd and NDVI sd). As detailed above, these mean values are the median pixel values within each buffer. EVI and NDVI mean values were strongly correlated with monthly values of EVI (Appendix S1: Figure S2) and NDVI (Appendix S1: Figure S3).

Facets of avian diversity assessment

A bird community is the total list of bird species present in each sample site. We assessed each bird community's different facets of avian diversity: taxonomic, functional, and phylogenetic diversity (Appendix S1: Table S2). The first facet corresponds to taxonomic diversity regarding BSR (Magurran, 2004). The second facet includes three metrics related to functional diversity: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Villéger et al., 2008). All functional diversity metrics were calculated through the "FD" package in R (Laliberté et al., 2015; Laliberté & Legendre, 2010) by using the avian niche database comprising 73 different traits (Pearman et al., 2014) (Appendix S1: Table S3). The third facet involves three metrics related to phylogenetic diversity: phylogenetic diversity (PD) (Faith, 1992), phylogenetic species variability (PSV) (Helmus et al., 2007), and community evolutionary distinctiveness (CED). We built the phylogenetic tree with the relationships among the species in each sample site, using genetic data from a total of 6663 taxa (Jetz et al., 2012), provided in BirdTree (https://birdtree.org/subsets/). PD and PSV metrics were estimated using the "picante"

package for R (Kembel et al., 2010). Finally, CED was assessed to determine the mean ED score for each bird community considering all species present (see details in Benedetti & Morelli, 2022) in a community (sample site) (Morelli et al., 2016; Tucker et al., 2016). We obtained the species ED score (Isaac et al., 2007; Redding et al., 2008) from the following online database: from https://www.edgeofexistence.org/edge-lists/ (Zoological Society of London, 2008).

Then, we calculated an urban tolerance mean (UTM) for every community (i.e., sample site) as species generally show responses to urbanization along a continuum. We used species-specific urban tolerance scores from Callaghan, Benedetti, et al., 2020. This method uses eBird citizen science data and VIIRS night-time lights to provide species-specific preferences for or against urbanization (for more details, see Callaghan, Major, et al., 2020). Then, we took the mean of the species-specific urban tolerance scores (UTM) across all species at that sample site (Appendix S1: Table S2).

Finally, we assessed avian specialization richness for each avian community (i.e., sample site). We used the avian species-specific specialization index estimated by Morelli et al., 2019 for different ecological traits: diet, foraging behavior, foraging substrate, and habitat (see details in Appendix S1: Table S3). The specialization richness in each sample site is estimated by the number of bird species with a specialization value equal to 1 (Benedetti et al., 2022; Morelli et al., 2019; Morelli, Benedetti, Hanson, & Fuller, 2021), see more details in Benedetti & Morelli, 2022. Thus, avian specialization richness types estimated were diet specialization richness (Diet), foraging behavior specialization richness (Forb), foraging substrate specialization richness (Forsub), and habitat specialization richness (Hab).

Statistical analyses

We explored EVI and NDVI values (mean and sd) associations with taxonomic, functional, and phylogenetic diversity, specialization types, and UTM. These associations were examined using Generalized Linear Mixed Models (GLMMs). Models were fitted by maximum likelihood using the package "nlme" and "lme4" in R (Bates et al., 2015; Pinheiro et al., 2019). Each diversity facet (Taxonomic diversity: Species richness; Functional diversity: Functional diversity, functional evenness, and functional divergence; Phylogenetic diversity: Phylogenetic diversity, phylogenetic species variability, and community evolutionary distinctiveness; UTM; and four specialization types: Diet, foraging behavior, foraging substrate, and habitat) (see detailed description in Appendix S1: Table S2) was established as a response variable and was

modeled separately. EVI and NDVI (mean and sd) were designated as predictors individually. They were modeled separately (each predictor for each response variable) since we aimed to evaluate the single capacity of EVI and NDVI (mean and sd) as surrogates of each avian diversity facet. EVI and NDVI mean showed a high level of collinearity (Appendix S1: Figure S3). The city was included as a random factor in the models. Geographical coordinates were not included as predictors, considering the redundancy of using cities as a random factor.

The response variables based on count data (e.g., BSR and all specialization richness types) were tested for overdispersion by employing the "aods3" package in R (Lesnoff & Lancelot, 2018). Therefore, a ratio between the sum of squared Pearson residuals and the residual degrees of freedom lower than one (<1) indicates no overdispersion issues (Agresti, 1990). Then, BSR and each type of specialization richness were modeled following a Poisson distribution. The normality assumptions of response variables based on continuous data (e.g., UTM, phylogenetic and functional diversity facets) were tested employing the "MASS" package (Venables & Ripley, 2002) in R. To normalize data not following a normal distribution, we log-transformed using the "rcompanion" package in R (Salvatore Mangiafico, 2021). Finally, the variables were modeled following a Gaussian distribution (Box & Cox, 1964).

The Akaike information criterion (AIC) was used to determine the "best" model explaining variation in the data of each significant model when exploring EVI or NDVI predictors (Burnham & Anderson, 2002). The model selection and multimodel inference were performed using the package "AICcmodavg" in R (Mazerolle, 2016). The model with the lowest AIC and greater Akaike information criterion weighted (AICWt) is considered the best model (Mazerolle, 2016). Thus, this study evaluated the best proxies' avian diversity facets among all EVI or NDVI indices explored.

Finally, the goodness of fit of each model was assessed by assessing the conditional R^2 (which considers the variance by the fixed and random effects) and marginal R^2 (which considers the variance by the fixed effects) using the function "rsquared" from the package "piecewiseSEM" (Lefcheck, 2016).

The correlation between predictors was performed using the "corrgram" function in R (Wright, 2018) to produce a matrix correlogram including the correlation value obtained by the Pearson correlation coefficient.

Confidence intervals for the significant variables selected in the best model were calculated by the Wald method using the "MASS" package in R (Venables & Ripley, 2002).

All modeling procedures, statistical tests, and data explorations were performed with R software v. 4.1.3

(R Development Core Team, 2019) and considered results statistically significant when the *p*-value was lower than 0.05.

RESULTS

In this study, 1382 sample sites were surveyed in 15 different European cities (Figure 1, Appendix S1: Table S1). A total of 113 avian species (see details in Benedetti & Morelli, 2022) and 31,760 individuals were recorded. The mean of total BSR across all 1382 sample sites was 7.23 species (minimum: 1, maximum: 24 species). The EVI mean values in 50-m buffers vary between 0.040 and 0.734, considering all sample sites. In contrast, the EVI sd values fluctuate between 0.006 and 0.248. NDVI mean values fluctuate between 0.048 and 0.684. At the same time, the NDVI sd values vary from 0.007 to 0.292. Considering only significant predictors, the values of conditional R^2 vary from 0.540 (for NDVI mean as a predictor of phylogenetic diversity [PD]) to 0.155 (for NDVI sd as a predictor of community evolutionary distinctiveness [CED]). The values of marginal R^2 ranged from 0.22 (for NDVI mean as a predictor of urban tolerance [UTM]) to 0.004 (for EVI sd and NDVI sd as predictors for habitat specialization richness [Hab]) (Appendix S1: Table S4).

EVI and NDVI as proxies of avian diversity

The number of species (BSR), functional richness (FRic), community evolutionary distinctiveness (CED), and phylogenetic diversity (PD) values of avian communities were positively associated with all indices investigated (e.g., EVI mean, EVI sd, NDVI mean, and NDVI sd). Conversely, phylogenetic species variability (PSV) was negatively associated (Table 1, Figure 2, Appendix S1: Figures S3–S6). In addition, functional divergence (FDiv) was not related to any EVI and NDVI indices used in this study, and functional evenness (FEve) was significantly related only to EVI and NDVI mean (Table 1, Figure 2, Appendix S1: Figures S3–S6). NDVI mean was the best proxy for BSR, FRic, FEve, CED, PD, and PSV as it carries between 99% and 67% of the cumulative model weight and has the lowest AIC (Table 1, Figure 2, Appendix S1: Figures S3–S6).

EVI and NDVI as proxies of avian urban tolerance

The UTM values were negatively associated with all indices, EVI and NDVI (both mean and sd). NDVI mean is

the selected best model, as it carries 99% of the cumulative model weight and has the lowest AIC score (Table 2, Figure 2, Appendix S1: Figures S3–S6).

EVI and NDVI as proxies of avian specialization

Bird assemblages characterized by a high number of diet (Diet), Foraging behavior (Forb), and Habitat (Hab) specialist species were positively associated with all indices investigated (e.g., EVI mean, EVI standard deviation, NDVI mean, and NDVI sd) (Table 3, Figure 2, Appendix S1: Figures S3–S6). Those areas characterized by the greater number of foraging substrate specialists (Forsub) were negatively related to EVI, and NDVI mean. NDVI mean was the best proxy for Diet, Forb, and Hab specialist species as it carries between 77 and 55% of the cumulative model weight and has the lowest AIC (Table 1, Figure 2, Appendix S1: Figures S3–S6). Finally, both EVI mean was the selected best model for Forsub, as it carries 69% of the cumulative model weight and has the lowest AIC score (Table 3, Figure 2, Appendix S1: Figures S3–S6).

DISCUSSION

Our analysis provides the first assessment investigating the ability of Landsat-derived EVI and NDVI as proxies of different facets of avian diversity (e.g., taxonomic, functional, and phylogenetic diversity, urban tolerance, and avian specialization) in urban landscapes across 15 European cities. We found that EVI mean as a surrogate of primary productivity was associated significantly with most avian diversity facets. However, EVI was the best predictor only for foraging substrate specialization. Specifically, EVI mean was negatively correlated to the number of bird species specialized in foraging substrate. Indicating a lower number of birds specialized in a particular foraging substrate are likely found in areas characterized by higher values of EVI mean. This finding could indicate a lower availability of potential foraging substrates (e.g., bare soil, artificial surfaces, and/or body water characterized) at higher cover vegetation. Most previous studies focused on the association between EVI (mean and standard deviation) and BSR (e.g., Callaghan, Major, et al., 2020; Cooper et al., 2020; Farwell et al., 2020; Hobi et al., 2017). Such studies were performed mainly in forest and rural areas (e.g., grassland and farmland). Instead, our findings are the first evidence that the EVI is significantly associated with multiple facets of avian diversity in urban areas and, most importantly, is the best predictor of foraging substrate specialization.

TABLE 1 Results of fixed-effect parameters in the GLMM model performed in this study, accounting for variations in the following diversity metrics: Bird species richness (BSR), Functional richness (FRic), Functional evenness (FEve), Functional divergence (FDiv), Community evolutionary distinctiveness (CED), Phylogenetic diversity (PD), and Phylogenetic species variability (PSV), concerning the following predictors: EVI mean, EVI standard deviation (EVI sd), NDVI mean, NDVI standard deviation (NDVI sd). Model = Individual models.
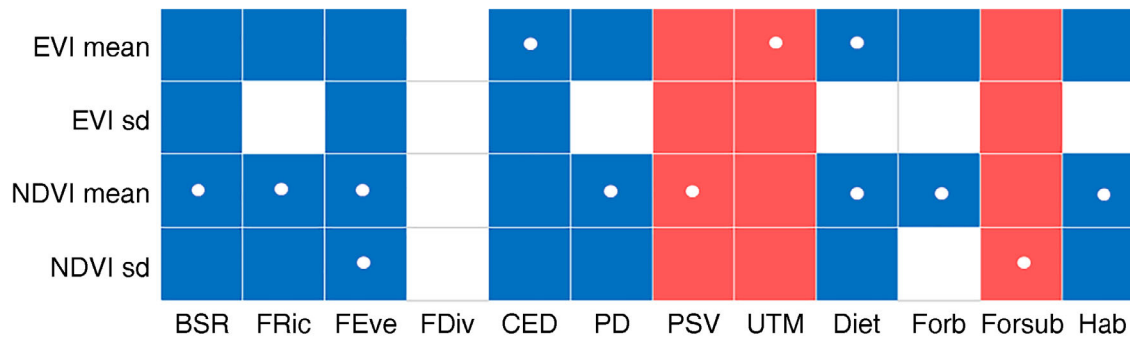
Model	ES	SE	t/z	p-value	AIC	Delta AIC	AICWt
Response variable: Bird species richness							
EVI mean	1.384	0.109	12.75	<0.001	3845.91	10.38	0.01
EVI sd	2.731	0.354	7.71	<0.001	3949.75	114.22	0
NDVI mean	**1.481**	**0.113**	**13.10**	**<0.001**	**3835.53**	**0**	**0.99**
NDVI sd	2.975	0.389	7.65	<0.001	3950.98	115.45	0
Response variable: Functional richness							
EVI mean	1.454	0.238	6.110	<0.001	2142.16	4.74	0.09
EVI sd	3.891	0.840	4.630	<0.001	2157.56	20.15	0
NDVI mean	**1.581**	**0.243**	**6.504**	**<0.001**	**2137.41**	**0**	**0.91**
NDVI sd	4.544	0.928	4.894	<0.001	2155.12	17.7	0
Response variable: Functional evenness							
EVI mean	0.437	0.052	8.458	<0.001	−598.88	5.86	0.05
EVI sd	0.459	0.177	2.587	0.0098	−537.29	67.45	0
NDVI mean	**0.467**	**0.053**	**8.834**	**<0.001**	**−604.77**	**0**	0.95
NDVI sd	0.306	0.197	1.558	0.1195	−533.07	71.67	0
Response variable: Functional divergence							
EVI mean	0.007	0.004	1.648	0.100	−4767.79	0.45	0.25
EVI sd	0.017	0.014	1.202	0.230	−4766.59	1.65	0.14
NDVI mean	**0.008**	**0.004**	**1.802**	**0.072**	**−4768.24**	**0**	**0.31**
NDVI sd	0.028	0.016	1.731	0.0839	−4768.11	0.13	0.30
Response variable: Community evolutionary distinctiveness							
EVI mean	0.073	0.006	12.815	<0.001	−4184.500	1.4	0.33
EVI sd	0.100	0.022	4.616	<0.001	−4055.203	130.7	0
NDVI mean	**0.075**	**0.006**	**12.880**	**<0.001**	**−4185.899**	**0**	**0.67**
NDVI sd	0.087	0.024	3.620	<0.001	−4047.140	138.8	0
Response variable: Phylogenetic diversity							
EVI mean	2.318	0.248	9.340	<0.001	2217.973	4.28	0.11
EVI sd	5.243	0.895	5.861	<0.001	2267.243	53.55	0
NDVI mean	**2.433**	**0.254**	**9.593**	**<0.001**	**2213.690**	**0**	**0.89**
NDVI sd	5.738	0.990	5.796	<0.001	2267.969	54.28	0
Response variable: Phylogenetic species variability							
EVI mean	−0.328	0.026	−12.550	<0.001	−1603.509	6.94	0.03
EVI sd	−0.459	0.098	−4.665	<0.001	−1480.491	129.95	0
NDVI mean	**−0.343**	**0.027**	**−12.877**	**<0.001**	**−1610.445**	**0**	**0.97**
NDVI sd	−0.391	0.110	−3.573	<0.001	−1471.652	138.79	0

Note: Each predictor was modeled separately for each response variable. The significant and selected model—according to the lowest AIC value and higher AICWt—is evidenced in bold. Additionally, conditional R^2 (variance explained by fixed and random effects) and marginal R^2 (variance explained by the fixed effects) assessed for each model are reported in Appendix S1: Table S4.

Abbreviations: AIC, Akaike information criterion; AICWt, Akaike information criterion weighted; ES, estimate; SE, standard error.

On the other hand, NDVI mean was significantly associated with most avian diversity facets. Specifically, it was positively correlated with BSR, functional richness, functional evenness, community evolutionary distinctiveness, phylogenetic diversity, and the number of diet and habitat specialists in urbanized areas. However, NDVI

FIGURE 2 Matrix representing the GLMM association types between avian diversity and community metrics and Landsat-derived indices. In the columns, the following responses variables are: Bird species richness (BSR), Functional richness (FRic), Functional evenness (FEve), Functional divergence (FDiv), Community evolutionary distinctiveness (CED), Phylogenetic diversity (PD), Phylogenetic species variability (PSV), Urban Tolerance mean (UTM), Diet specialization richness (Diet), Foraging behavior specialization richness (Forb), Foraging substrate specialization richness (Forsub), Habitat specialization richness (Hab). In the rows, the following predictive variables are: EVI mean, EVI standard deviation (EVI sd), NDVI mean, and NDVI standard deviation (NDVI sd). Each predictive variable was assessed in separate models. Blue squares represent positive and significant associations. Red squares represent negative and significant associations. White squares represent non-significant associations. The selected best models—according to the lowest AIC and greater AICWt values—are indicated with a white dot. See detailed results in Tables 1–3.

TABLE 2 Results of fixed-effect parameters in the GLMM model performed in this study, accounting for variations in Urban Tolerance mean (UTM), concerning the following predictors: EVI mean, EVI standard deviation (EVI sd), NDVI mean, NDVI standard deviation (NDVI sd).

Model	ES	SE	t/z	p-value	AIC	Delta AIC	AICWt
Response variable: Urban tolerance mean							
EVI mean	−4.380	0.221	−19.854	<0.001	3961.821	9.70	0.01
EVI sd	−7.251	0.855	−8.479	<0.001	4237.844	285.72	0
NDVI mean	**−4.605**	**0.228**	**−20.176**	**<0.001**	**3952.123**	**0**	**0.99**
NDVI sd	−6.394	0.980	−6.524	<0.001	4265.989	313.87	0

Note: Model, Individual models. Each predictor was modeled separately for each response variable. The significant and selected model—according to the lowest AIC value and higher AICWt—is evidenced in bold. Additionally, conditional R^2 (variance explained by fixed and random effects) and marginal R^2 (variance explained by the fixed effects) assessed for each model are reported in Appendix S1: Table S4.
Abbreviations: AIC, Akaike information criterion; AICWt, Akaike information criterion weighted; ES, estimate; SE, standard error.

mean was correlated negatively to phylogenetic species variability, urban tolerance, and foraging substrate specialism. Simultaneously, except for foraging substrate specialization, NDVI mean was the best predictor of all avian diversity metrics explored in this study. Hence, urban areas with high NDVI mean values were characterized by a greater number of bird species (Ibáñez-Álamo et al., 2016), high functional richness, and phylogenetical diversity (Morelli, Benedetti, Ibáñez-Álamo, et al., 2021), and also a greater number of avian specialists. In agreement, previous studies found higher species richness and phylogenetic diversity associated with low-density urban areas, which we can assume greater NDVI mean values (Ibáñez-Álamo et al., 2016; Morelli et al., 2016; Morelli, Benedetti, Ibáñez-Álamo, et al., 2021). Conversely, in areas with high values of NDVI mean, avian assemblages were barely correlated phylogenetically and with few urban tolerant species and foraging substrate specialists. Our results show that a greater vegetation cover supports urban areas with avian assemblages taxonomically less related and with a greater number of native species. Therefore, greater NDVI mean values can identify urban areas with lower avian biotic homogenization (Morelli, Benedetti, Ibáñez-Álamo, et al., 2021). Accordingly, most studies focused on NDVI as a proxy of avian diversity found positive associations between NDVI and BSR and functional diversity (Bailey et al., 2004; Gillespie, 2005; Hurlbert & Haskell, 2003; Levin et al., 2007; Seto et al., 2004). Leveau et al. (2020) found a negative correlation between NDVI and community evolutionary distinctiveness in Argentine, contrasting our findings. Such discrepancies could be associated with the sampling size differences between both studies or the bird species composing such avian assemblages. For example, the overall

TABLE 3 Results of fixed-effect parameters in the GLMM model performed in this study, accounting for variations in each category of specialization richness: Diet (Diet), Foraging behavior (Forb), Foraging substrate (Forsub), and Habitat (Hab) concerning the following predictors: EVI mean, EVI standard deviation (EVI sd), NDVI mean, NDVI standard deviation (NDVI sd).

Model	ES	SE	t/z	p-Value	AIC	Delta AIC	AICWt
Response variable: Diet richness							
EVI mean	0.857	0.180	4.750	<0.001	3823.02	0.46	0.44
EVI sd	2.276	0.610	3.735	<0.001	3831.9	9.34	0.01
NDVI mean	**0.905**	**0.189**	**4.784**	**<0.001**	**3822.56**	**0**	**0.55**
NDVI sd	2.405	0.688	3.498	<0.001	3833.59	11.03	0
Response variable: Foraging behavior richness							
EVI mean	0.696	0.133	5.123	<0.001	4678.76	0.48	0.28
EVI sd	2.197	0.430	5.110	<0.001	4680.38	2.11	0.12
NDVI mean	**0.733**	**0.140**	**5.248**	**<0.001**	**4678.28**	**0**	**0.35**
NDVI sd	2.555	0.486	5.255	<0.001	4679.02	0.74	0.24
Response variable: Foraging substrate richness							
EVI mean	**−0.694**	**0.182**	**−3.806**	**<0.001**	**3715.79**	**0**	**0.69**
EVI sd	−0.517	0.616	−0.840	0.4008	3729.63	13.84	0
NDVI mean	−0.678	0.189	−3.595	<0.001	3717.42	1.63	0.31
NDVI sd	0.006	0.691	0.009	0.993	3730.34	14.55	0
Response variable: Habitat richness							
EVI mean	1.424	0.294	4.844	<0.001	2356.12	2.41	0.23
EVI sd	3.358	0.880	3.815	<0.001	2365.31	11.59	0
NDVI mean	**1.590**	**0.314**	**5.072**	**<0.001**	**2353.72**	**0**	**0.77**
NDVI sd	3.817	1.001	3.795	<0.001	2365.5	11.79	0

Note: Model, Individual models. Each predictor was modeled separately for each response variable. The significant and selected model—according to the lowest AIC value and higher AICWt—is evidenced in bold. Additionally, conditional R^2 (variance explained by fixed and random effects) and marginal R^2 (variance explained by the fixed effects) assessed for each model are reported in Appendix S1: Table S4.

Abbreviations: AIC, Akaike information criterion; AICWt, Akaike information criterion weighted; ES, estimate; SE, standard error.

avian assemblages in European cities can be characterized by higher community evolutionary distinctiveness than those found in Argentine (Ibáñez-Álamo et al., 2016; Morelli et al., 2016). These differences can be related to the presence of *Upupa epops* in some urban areas, a species characterized by a high evolutionary distinctiveness score.

Our findings indicate that the mean values of NDVI and EVI are suitable as proxies for monitoring different facets of avian diversity in urban areas. However, NDVI mean was the best predictor for most avian diversity metrics. Considering that both vegetation indices are surrogates of primary productivity (Huete, Didan, Miura, Rodriguez, Gao, & Ferreira, 2002), these findings are consistent with the species-energy hypothesis (Wright, 1983). Such a hypothesis claims that the species diversity of vertebrates (including birds) and invertebrates should increase with energy availability (Evans & Gaston, 2005; Hawkins, Field, et al., 2003; Lennon et al., 2004). Accordingly, our results show that areas at high productivity levels (greater vegetation biomass), represented by high EVI and NDVI values, support avian assemblages with a high number of native species, more diverse functionally, less related phylogenetically, and more distinctive species. Therefore, in such areas, we can expect a greater number of avian specialist species, particularly in diet and foraging behavior.

Regarding vegetation heterogeneity, several studies demonstrated the ability of EVI sd and NDVI sd to represent vegetation heterogeneity (Seto et al., 2004). Similar to EVI and NDVI mean, our results showed that EVI sd and NDVI sd were significantly and positively associated with most avian diversity facets. Instead, they were negatively correlated to phylogenetic species variability and urban tolerance. We expected such results because heterogeneous environments provide a greater diversity of microhabitats and niches potentially suitable as refugia, substrate, and other resources for the organisms (Keppel et al., 2011; Stein et al., 2014; Tews et al., 2004). Nonetheless, EVI sd and NDVI sd were not the best predictors for any avian diversity facets studied since they exhibited an overall lower performance than the other predictors.

CONCLUDING REMARKS AND PERSPECTIVES

Previous studies demonstrated that each satellite sensor (e.g., Landsat, Sentinel, or Gaofen) provides different vegetation indices values. Such differences can affect the accuracy of the assessment of the vegetation attributes (Wu et al., 2020; Zhao et al., 2018). The search for the "best" proxy should consider the trade-offs among vegetation index effectiveness, economic costs, and spatiotemporal resolution for each band and sensor type. Therefore, further studies could apply this framework by exploring other potential proxies of avian diversity metrics by using spectral indices based on other bands such as SWIR band (e.g., NDWI, Normalized Difference Water Index) or linear band transformations (e.g., TCT, Tasseled Caps Transformation), and by also examining different satellite sensors (e.g., Sentinel-2A, Sentinel-2B, WorldView-2). Additionally, we encourage that upcoming studies should expand the temporal monitoring scheme to detect changes in avian assemblages of urban areas.

The World Cities Report 2020 (United Nations Human Settlements Programme, 2022), jointly with the New Urban Agenda (United Nations, 2017) and the European Biodiversity Strategy for 2030 (EC, 2020), recognizes the value of urban green areas in removing carbon from the atmosphere and safeguarding biodiversity. Such programs call for different measures to promote green space areas, increasing environmental resilience in human settlements. Accordingly, our results indicate that greater cover of green areas can support different facets of urban avian diversity. For this reason, efficient conservation strategies in cities should be considered: (1) Maintaining different types of green-area habitats, not only forests and urban parks (Nguyen et al., 2020), but also larger urban greenspaces to preserve connectivity in the city (Callaghan et al., 2018; EC, 2020; Nguyen et al., 2020; United Nations, 2017); and (2) Restoring vegetation cover to support avian communities confronting climate change (EC, 2020). Additionally, we recommend long-term and broader spatial monitoring of different avian diversity metrics in urban areas using NDVI mean to detect temporal and spatial changes in avian assemblages. Therefore, such approaches can help to explore the potential vulnerabilities of bird assemblages facing climatic and land-use changes and promote more efficient landscape restoration and urban planning, congruently with biodiversity conservation.

In summary, we tested the efficiency of remote sensing measurements as proxies' of multiple facets of avian diversity using data from several European cities, considering that: (1) most articles focusing on vegetation indices and avian diversity metrics are based on single-city studies; (2) assess proxies of avian diversity in urban areas is essential given that the spectral indices can find different technical limitations (e.g., higher reflectance from different material types) if compared to natural or rural areas (Xue & Su, 2017); and (3) several facets of avian diversity were not previously assessed (e.g., phylogenetic relatedness, urban tolerance, and different specialization traits of avian assemblages) even though they can mirror undetected biotic homogenization (Petchey & Gaston, 2006). Our findings showed that although all vegetation indices explored in this study were significantly related to most avian diversity facets, NDVI mean was the best explanatory vegetation index for avian diversity in urban areas.

CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

EVI and NDVI data were calculated using the USGS Landsat 8 Collection 1 Tier 1 imagery from the Google Earth Engine catalog: https://developers.google.com/earth-engine/datasets/catalog/LANDSAT_LC08_C02_T1_RT_TOA. The avian niche database, comprising 73 different traits, was obtained from Pearman et al. (2014) and is available in the supplementary material at https://onlinelibrary.wiley.com/doi/10.1111/geb.12127. Phylogeny data for birds were downloaded from BirdTree https://birdtree.org/subsets/ using the list avian species subset from Benedetti and Morelli (2022) in Figshare at https://doi.org/10.6084/m9.figshare.19780285.v1. Evolutionary distinctiveness score for birds were downloaded from https://www.edgeofexistence.org/edge-lists/ by searching for "ED scores–birds". Species specific urban tolerance scores were

downloaded from Callaghan, Benedetti, et al. (2020) and are available in the supplementary material provided at https://www.oikosjournal.org/appendix/oik-07356. Bird specialization data was extracted from Morelli et al. (2019) and are also available in Benedetti and Morelli (2022) in Figshare at https://doi.org/10.6084/m9.figshare.19780285.v1.

ORCID

Yanina Benedetti https://orcid.org/0000-0003-1600-2310

Corey T. Callaghan https://orcid.org/0000-0003-0415-2709

Farah Abou Zeid https://orcid.org/0000-0002-0686-143X

Piotr Tryjanowski https://orcid.org/0000-0002-8358-0797

REFERENCES

Agresti, A. 1990. *Categorical Data Analysis*. Hoboken: Wiley.

Arenas-Castro, S., A. Regos, J. F. Gonçalves, D. Alcaraz-Segura, and J. Honrado. 2019. "Remotely Sensed Variables of Ecosystem Functioning Support Robust Predictions of Abundance Patterns for Rare Species." *Remote Sensing* 11: 2086.

Bacaro, G., E. Santi, D. Rocchini, F. Pezzo, L. Puglisi, and A. Chiarucci. 2011. "Geostatistical Modelling of Regional Bird Species Richness: Exploring Environmental Proxies for Conservation Purpose." *Biodiversity and Conservation* 20: 1677–94.

Bae, S., J. Müller, D. Lee, K. T. Vierling, J. C. Vogeler, L. A. Vierling, A. T. Hudak, H. Latifi, and S. Thorn. 2018. "Taxonomic, Functional, and Phylogenetic Diversity of Bird Assemblages Are Oppositely Associated to Productivity and Heterogeneity in Temperate Forests." *Remote Sensing of Environment* 215: 145–56.

Bailey, S. A., M. C. Horner-Devine, G. Luck, L. A. Moore, K. M. Carney, S. Anderson, C. Betrus, and E. Fleishman. 2004. "Primary Productivity and Species Richness: Relationships among Functional Guilds, Residency Groups and Vagility Classes at Multiple Spatial Scales." *Ecography* 27: 207–17.

Bässler, C., M. Cadotte, B. Beudert, C. Heibl, M. Blaschke, J. Bradtka, T. Langbehn, S. Werth, and J. Müller. 2016. "Contrasting Patterns of Lichen Functional Diversity and Species Richness across an Elevation Gradient." *Ecography* 39: 689–98.

Batáry, P., K. Kurucz, M. Suarez-Rubio, and D. E. Chamberlain. 2018. "Non-linearities in Bird Responses across Urbanization Gradients: A Meta-Analysis." *Global Change Biology* 24: 1046–54.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Benedetti, Y., and F. Morelli. 2022. "List of Avian Species.Xlsx." Figshare. Dataset.

Benedetti, Y., F. Morelli, C. T. Callaghan, and R. Fuller. 2022. "Distribution and Protection of Avian Specialization in Europe." *Global Ecology and Biogeography* 31: 10–24.

Bergen, K. M., A. M. Gilboy, and D. G. Brown. 2007. "Multi-dimensional Vegetation Structure in Modeling Avian Habitat." *Ecological Informatics* 2: 9–22.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. *Bird Census Techniques (Google eBook)*. Cambridge: Academic Press.

Bino, G., N. Levin, S. Darawshi, N. van der Hal, A. Reich-Solomon, and S. Kark. 2008. "Accurate Prediction of Bird Species Richness Patterns in an Urban Environment Using Landsat-Derived NDVI and Spectral Unmixing." *International Journal of Remote Sensing* 29: 3675–700.

Blair, R. B. 1996. "Land Use and Avian Species Diversity along an Urban Gradient." *Ecological Applications* 6: 506–19.

Boles, S. H., X. Xiao, J. Liu, Q. Zhang, S. Munkhtuya, S. Chen, and D. Ojima. 2004. "Land Cover Characterization of Temperate East Asia Using Multi-Temporal Vegetation Sensor Data." *Remote Sensing of Environment* 90: 477–89.

Bonthoux, S., S. Lefèvre, P. A. Herrault, and D. Sheeren. 2018. "Spatial and Temporal Dependency of NDVI Satellite Imagery in Predicting Bird Diversity over France." *Remote Sensing* 10: 1–22.

Box, E. O., B. N. Holben, and V. Kalb. 1989. "Accuracy of the AVHRR Vegetation Index as a Predictor of Biomass, Primary Productivity and Net CO2 Flux." *Vegetatio* 80: 71–89.

Box, G. E. P., and D. R. Cox. 1964. "An Analysis of Transformations." *Journal of the Royal Statistical Society (B)* 26: 211–52.

Brooks, T. M., R. A. Mittermeier, J. da Fonseca, G. A. B. Gerlach, J. F. Hoffmann, M. Lamoreux, C. G. Mittermeier, D. Pilgrim, and A. S. L. Rodrigues. 2006. "Global Biodiversity Conservation Priorities." *Science* 313: 58–61.

Burnham, K. K. P., and D. D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. New York: Springer.

Callaghan, C. T., Y. Benedetti, J. H. Wilshire, and F. Morelli. 2020. "Avian Trait Specialization Is Negatively Associated with Urban Tolerance." *Oikos* 129: 1541–51.

Callaghan, C. T., R. E. Major, W. K. Cornwell, A. G. B. Poore, J. H. Wilshire, and M. B. Lyons. 2020. "A Continental Measure of Urbanness Predicts Avian Response to Local Urbanization." *Ecography* 43: 528–38.

Callaghan, C. T., R. E. Major, M. B. Lyons, J. M. Martin, and R. T. Kingsford. 2018. "The Effects of Local and Landscape Habitat Attributes on Bird Diversity in Urban Greenspaces." *Ecosphere* 9: e02347.

Carmona, C. P., F. M. Azcárate, F. de Bello, H. S. Ollero, J. Lepš, and B. Peco. 2012. "Taxonomical and Functional Diversity Turnover in Mediterranean Grasslands: Interactions between Grazing, Habitat Type and Rainfall." *Journal of Applied Ecology* 49: 1084–93.

Caruso, G., L. Tozzini, G. Rallo, J. Primicerio, M. Moriondo, G. Palai, and R. Gucci. 2017. "Estimating Biophysical and Geometrical Parameters of Grapevine Canopies ("Sangiovese") by an Unmanned Aerial Vehicle (UAV) and VIS-NIR Cameras." *Vitis - Journal of Grapevine Research* 56: 63–70.

Clavel, J., R. Julliard, and V. Devictor. 2011. "Worldwide Decline of Specialist Species: Toward a Global Functional Homogenization?" *Frontiers in Ecology and Environment* 9: 222–8.

Cooper, W. J., W. J. McShea, T. Forrester, and D. A. Luther. 2020. "The Value of Local Habitat Heterogeneity and Productivity when Estimating Avian Species Richness and Species of Concern." *Ecosphere* 11: e03107.

Coops, N. C., R. H. Waring, M. A. Wulder, A. M. Pidgeon, and V. C. Radeloff. 2009. "Bird Diversity: A Predictable Function of Satellite-Derived Estimates of Seasonal Variation in Canopy

Light Absorbance across the United States." *Journal of Biogeography* 36: 905–18.

Cramer, W., D. W. Kicklighter, A. Bondeau, B. Moore, G. Churkina, B. Nemry, A. Ruimy, and A. L. Schloss. 1999. "Comparing Global Models of Terrestrial Net Primary Productivity (NPP): Overview and Key Results." *Global Change Biology* 5: 1–15.

Croci, S., A. Butet, A. Georges, R. Aguejdad, and P. Clergeau. 2008. "Small Urban Woodlands as Biodiversity Conservation Hot-Spot: A Multi-Taxon Approach." *Landscape Ecology* 23: 1171–86.

Culbert, P. D., V. C. Radeloff, V. St-Louis, C. H. Flather, C. D. Rittenhouse, T. P. Albright, and A. M. Pidgeon. 2012. "Modeling Broad-Scale Patterns of Avian Species Richness across the Midwestern United States with Measures of Satellite Image Texture." *Remote Sensing of Environment* 118: 140–50.

Davi, H., K. Soudani, T. Deckx, E. Dufrene, V. le Dantec, and C. François. 2006. "Estimation of Forest Leaf Area Index from SPOT Imagery Using NDVI Distribution over Forest Stands." *International Journal of Remote Sensing* 27: 885–902.

Davies, K. F., C. R. Margules, and J. F. Lawrence. 2004. "A Synergistic Effect Puts Rare, Specialized Species at Greater Risk of Extinction." *Ecology* 85: 265–71.

Dehling, D. M., S. A. Fritz, T. Töpfer, M. Päckert, P. Estler, K. Böhning-Gaese, and M. Schleuning. 2014. "Functional and Phylogenetic Diversity and Assemblage Structure of Frugivorous Birds along an Elevational Gradient in the Tropical Andes." *Ecography* 37: 1047–55.

Devictor, V., R. Julliard, D. Couvet, A. Lee, and F. Jiguet. 2007. "Functional Homogenization Effect of Urbanization on Bird Communities." *Conservation Biology* 21: 741–51.

Devictor, V., R. Julliard, and F. Jiguet. 2008. "Distribution of Specialist and Generalist Species along Spatial Gradients of Habitat Disturbance and Fragmentation." *Oikos* 117: 507–14.

Devictor, V., D. Mouillot, C. N. Meynard, F. Jiguet, W. Thuiller, and N. Mouquet. 2010. "Spatial Mismatch and Congruence between Taxonomic, Phylogenetic and Functional Diversity: The Need for Integrative Conservation Strategies in a Changing World." *Ecology Letters* 13: 1030–40.

Dobson, L. L., F. A. la Sorte, L. L. Manne, and B. A. Hawkins. 2015. "The Diversity and Abundance of North American Bird Assemblages Fail to Track Changing Productivity." *Ecology* 96: 1105–14.

Ducatez, S., J. Clavel, and L. Lefebvre. 2015. "Ecological Generalism and Behavioural Innovation in Birds: Technical Intelligence or the Simple Incorporation of New Foods?" *Journal of Animal Ecology* 84: 79–89.

Dutrieux, L. P., J. Verbesselt, L. Kooistra, and M. Herold. 2015. "Monitoring Forest Cover Loss Using Multiple Data Streams, a Case Study of a Tropical Dry Forest in Bolivia." *ISPRS Journal of Photogrammetry and Remote Sensing* 107: 112–25.

EC. 2020. "Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. EU Biodiversity Strategy for 2030." Bringing nature back into our lives. Brussels, 20.5.2020.COM.

Evans, K. L., and K. J. Gaston. 2005. "People, Energy and Avian Species Richness." *Global Ecology and Biogeography* 14: 187–96.

Evans, K. L., S. E. Newson, and K. J. Gaston. 2009. "Habitat Influences on Urban Avian Assemblages." *Ibis* 151: 19–39.

Faith, D. P. 1992. "Conservation Evaluation and Phylogenetic Diversity." *Biological Conservation* 61: 1–10.

Farwell, L. S., P. R. Elsen, E. Razenkova, A. M. Pidgeon, and V. C. Radeloff. 2020. "Habitat Heterogeneity Captured by 30-m Resolution Satellite Image Texture Predicts Bird Richness across the United States." *Ecological Applications* 30: e02157.

Foody, G. M., and M. E. J. Cutler. 2006. "Mapping the Species Richness and Composition of Tropical Forests from Remotely Sensed Data with Neural Networks." *Ecological Modelling* 195: 37–42.

Gao, X., A. R. Huete, W. Ni, and T. Miura. 2000. "Optical-Biophysical Relationships of Vegetation Spectra without Background Contamination." *Remote Sensing of Environment* 74: 609–20.

Gillespie, T. W. 2005. "Predicting Woody-Plant Species Richness in Tropical Dry Forests: A Case Study from South Florida, USA." *Ecological Applications* 15: 27–37.

Gonsamo, A. 2010. "Leaf Area Index Retrieval Using Gap Fractions Obtained from High Resolution Satellite Data: Comparisons of Approaches, Scales and Atmospheric Effects." *International Journal of Applied Earth Observation and Geoinformation* 12: 233–48.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. "Google Earth Engine: Planetary-Scale Geospatial Analysis for Everyone." *Remote Sensing of Environment* 202: 18–27.

Gould, W. 2000. "Remote Sensing of Vegetation, Plant Species Richness, and Regional Biodiversity Hotspots." *Ecological Applications* 10: 1861–70.

Grass, I., R. Brandl, A. Botzat, E. L. Neuschulz, and N. Farwig. 2015. "Contrasting Taxonomic and Phylogenetic Diversity Responses to Forest Modifications: Comparisons of Taxa and Successive Plant Life Stages in South African Scarp Forest." *PLoS One* 10: e0118722.

Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu, X. Bai, and J. M. Briggs. 2008. "Global Change and the Ecology of Cities." *Science* 319: 756–60.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J. F. Guégan, D. M. Kaufman, J. T. Kerr, et al. 2003. "Energy, Water, and Broad-Scale Geographic Patterns of Species Richness." *Ecology* 84: 3105–17.

Hawkins, B. A., E. E. Porter, and J. A. F. Diniz-Filho. 2003. "Productivity and History as Predictors of the Latitudinal Diversity Gradient of Terrestrial Birds." *Ecology* 84: 1608–23.

Helmus, M. R., T. J. Bland, C. K. Williams, and A. R. Ives. 2007. "Phylogenetic Measures of Biodiversity." *The American Naturalist* 169: E68–83.

Hobi, M. L., M. Dubinin, C. H. Graham, N. C. Coops, M. K. Clayton, A. M. Pidgeon, and V. C. Radeloff. 2017. "A Comparison of Dynamic Habitat Indices Derived from Different MODIS Products as Predictors of Avian Species Richness." *Remote Sensing of Environment* 195: 142–52.

Holben, B. N. 1986. "Characteristics of Maximum-Value Composite Images from Temporal AVHRR Data." *International Journal of Remote Sensing* 7: 1417–34.

Huang, S., L. Tang, J. P. Hupy, Y. Wang, and G. Shao. 2021. "A Commentary Review on the Use of Normalized Difference Vegetation Index (NDVI) in the Era of Popular Remote Sensing." *Journal of Forestry Research* 32: 1–6.

Huete, A., K. Didan, T. Miura, E. Rodriguez, X. Gao, and L. G. Ferreira. 2002. "Overview of the Radiometric and Biophysical

Performance of the MODIS Vegetation Indices." *Remote Sensing of Environment* 83: 195–213.

Huete, A. R. 1988. "A soil-adjusted vegetation index (SAVI)." *Remote Sensing of Environment* 25: 295–309.

Huete, A. R., and C. Justice. 1999. "MODIS Vegetation Index (MOD13) Algorithm Theoretical Basis Document Version 3.1 Principal Investigators."

Hurlbert, A. H., and J. P. Haskell. 2003. "The Effect of Energy and Seasonality on Avian Species Richness and Community Composition." *American Naturalist* 161: 83–97.

Ibáñez-Álamo, J. D., E. Rubio, Y. Benedetti, and F. Morelli. 2016. "Global Loss of Avian Evolutionary Uniqueness in Urban Areas." *Global Change Biology* 23: 2990–8.

Ibarra, J. T., S. Tom, and K. Martin. 2015. "Biotic Homogenization: Loss of Avian Functional Richness and Habitat Specialists in Disturbed Andean Temperate Forests." *Biological Conservation* 192: 418–27.

Irschick, D., L. Dyer, and T. W. Sherry. 2005. "Phylogenetic Methodologies for Studying Specialization." *Oikos* 110: 404–8.

Isaac, N. J. B., S. T. Turvey, B. Collen, C. Waterman, and J. E. M. Baillie. 2007. "Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny." *PLoS One* 2: e296.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. "The Global Diversity of Birds in Space and Time." *Nature* 491: 444–8.

Jiang, Z., A. R. Huete, K. Didan, and T. Miura. 2008. "Development of a Two-Band Enhanced Vegetation Index without a Blue Band." *Remote Sensing of Environment* 112: 3833–45.

Jokimäki, J., and J. Suhonen. 1993. "Effects of Urbanization on the Breeding Bird Species Richness in Finland: A Biogeographical Comparison." *Ornis Fennica* 70: 71–7.

Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, C. O. Webb, C. O. Webb, and C. O. Webb. 2010. "Picante: R Tools for Integrating Phylogenies and Ecology." *Bioinformatics* 26: 1463–4.

Keppel, G., K. Van Niel, G. Wardell-Johnson, C. Yates, M. Byrne, L. Mucina, A. Schut, S. Hopper, and S. Franklin. 2011. "Refugia: Identifying and Understanding Safe Havens for Biodiversity under Climate Change." *Global Ecology Biogeography* 21: 393–404.

Kéry, M., J. A. Royle, and H. Schmid. 2005. "Modeling Avian Abundance from Replicated Counts Using Binomial Mixture Models." *Ecological Applications* 15: 1450–61.

Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91: 299–305.

Laliberté, E., P. Legendre, and B. Shipley. 2015. "Measuring Functional Diversity (FD) from Multiple Traits, and Other Tools for Functional Ecology: R Package Version 1.0-12." *CRAN*.

Lassau, S. A., G. Cassis, P. K. J. Flemons, L. Wilkie, and D. F. Hochuli. 2005. "Using High-Resolution Multi-Spectral Imagery to Estimate Habitat Complexity in Open-Canopy Forests: Can we Predict Ant Community Patterns?" *Ecography* 28: 495–504.

Lausch, A., L. Bannehr, M. Beckmann, C. Boehm, H. Feilhauer, J. M. Hacker, M. Heurich, et al. 2016. "Linking Earth Observation and Taxonomic, Structural and Functional Biodiversity: Local to Ecosystem Perspectives." *Ecological Indicators* 70: 317–39.

Lee, T. M., and W. Jetz. 2008. "Future Battlegrounds for Conservation under Global Change." *Proceedings of the Royal Society London B* 275: 1261–70.

Lefcheck, J. S. 2016. "piecewiseSEM: Piecewise Structural Equation Modelling in r for Ecology, Evolution, and Systematics." *Methods in Ecology and Evolution* 7: 573–9.

Lennon, J. J., P. Koleff, J. J. D. Greenwood, and K. J. Gaston. 2004. "Contribution of Rarity and Commonness to Patterns of Species Richness." *Ecology Letters* 7: 81–7.

Lesnoff, M., and R. Lancelot. 2018. "aods3: Analysis of Overdispersed Data Using S3 Methods."

Leveau, C. M., and L. M. Leveau. 2005. "Avian Community Response to Urbanization in the Pampean Region, Argentina." *Ornitologia Neotropical* 16: 503–1.

Leveau, L. M. 2019. "Primary Productivity and Habitat Diversity Predict Bird Species Richness and Composition along Urban-Rural Gradients of Central Argentina." *Urban Forestry and Urban Greening* 43: 126349.

Leveau, L. M., F. I. Isla, and M. I. Bellocq. 2018. "Predicting the Seasonal Dynamics of Bird Communities along an Urban-Rural Gradient Using NDVI." *Landscape and Urban Planning* 177: 103–13.

Leveau, L. M., F. I. Isla, and M. Isabel Bellocq. 2020. "From Town to Town: Predicting the Taxonomic, Functional and Phylogenetic Diversity of Birds Using NDVI." *Ecological Indicators* 119: 106703.

Levin, N., A. Shmida, O. Levanoni, H. Tamari, and S. Kark. 2007. "Predicting Mountain Plant Richness and Rarity from Space Using Satellite-Derived Vegetation Indices." *Diversity and Distributions* 13: 692–703.

Lin, H. T., C. Y. Sun, and C. T. Hung. 2008. "A Study in the Relationship between Greenery of Urban Parks and Bird Diversity in Tainan City, Taiwan." *WIT Transactions on Ecology and the Environment* 117: 193–202.

Liu, H. Q., and A. Huete. 2019. "A Feedback Based Modification of the NDVI to Minimize Canopy Background and Atmospheric Noise." *IEEE Transactions on Geoscience and Remote Sensing* 33: 457–65.

Liu, J., O. J. Sun, H. Jin, Z. Zhou, and X. Han. 2011. "Application of Two Remote Sensing GPP Algorithms at a Semiarid Grassland Site of North China." *Journal of Plant Ecology* 4: 302–12.

MacArthur, R. H., and J. W. MacArthur. 1961. "On Bird Species Diversity." *Ecology* 42: 594–8.

Magurran, A. 2004. *Measuring Biological Diversity*. Oxford: Blackwell.

Marzluff, J. M. 2001. "Worldwide Urbanization and Its Effect on Birds." Avian Ecology and Conservation in an Urbanizing World: 4615.

Matsushita, B., W. Yang, J. Chen, Y. Onda, and G. Qiu. 2007. "Sensitivity of the Enhanced Vegetation Index (EVI) and Normalized Difference Vegetation Index (NDVI) to Topographic Effects: A Case Study in High-Density Cypress Forest." *Sensors* 7: 2636–51.

Mazerolle, M. J. 2016. "AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c)." R package version 2.0-4.

Mcfarland, T. M., C. van Riper, and G. E. Johnson. 2012. "Evaluation of NDVI to Assess Avian Abundance and Richness along the Upper San Pedro River." *Journal of Arid Environments* 77: 45–53.

McKinney, M. L. 2002. "Urbanization, Biodiversity, and Conservation." *Bioscience* 52: 883–90.

McKinney, M. L. 2006. "Urbanization as a Major Cause of Biotic Homogenization." *Biological Conservation* 127: 247–60.

McKinney, M. L., and J. L. Lockwood. 1999. "Biotic Homogenization: A Few Winners Replacing Many Losers in the Nextmass Extinction." *Trends Ecology Evolution* 14: 450–3.

Melles, S., S. Glenn, and K. Martin. 2003. "Urban Bird Diversity and Landscape Complexity: Species-Environment Associations along a Multiscale Habitat Gradient." *Ecology and Society* 7: 070105.

Mildrexler, D. J., M. Zhao, and S. W. Running. 2009. "Testing a MODIS Global Disturbance Index across North America." *Remote Sensing of Environment* 113: 2103–17.

Morelli, F., Y. Benedetti, J. O. Hanson, and R. A. Fuller. 2021. "Global Distribution and Conservation of Avian Diet Specialization." *Conservation Letters* 14: e12795.

Morelli, F., Y. Benedetti, J. D. Ibáñez-Álamo, J. Jokimäki, R. Mänd, P. Tryjanowski, and A. P. Møller. 2016. "Evidence of Evolutionary Homogenization of Bird Communities in Urban Environments across Europe." *Global Ecology and Biogeography* 25: 1284–93.

Morelli, F., Y. Benedetti, J. D. Ibáñez-Álamo, P. Tryjanowski, J. Jokimäki, M.-L. Kaisanlahti-Jokimäki, J. Suhonen, et al. 2021. "Effects of Urbanization on Taxonomic, Functional and Phylogenetic Avian Diversity in Europe." *Science of the Total Environment* 795: 148874.

Morelli, F., Y. Benedetti, A. P. Møller, and R. A. Fuller. 2019. "Measuring Avian Specialization." *Ecology and Evolution* 9: 8378–86.

Muraoka, H., H. M. Noda, S. Nagai, T. Motohka, T. M. Saitoh, K. N. Nasahara, and N. Saigusa. 2013. "Spectral Vegetation Indices as the Indicator of Canopy Photosynthetic Productivity in a Deciduous Broadleaf Forest." *Journal of Plant Ecology* 6: 393–407.

Nagler, P. L., R. L. Scott, C. Westenburg, J. R. Cleverly, E. P. Glenn, and A. R. Huete. 2005. "Evapotranspiration on Western US Rivers Estimated Using the Enhanced Vegetation Index from MODIS and Data from Eddy Covariance and Bowen Ratio Flux Towers." *Remote Sensing of Environment* 97: 337–51.

Nguyen, T. T., P. Barber, R. Harper, T. V. K. Linh, and B. Dell. 2020. "Vegetation Trends Associated with Urban Development: The Role of Golf Courses." *PLoS One* 15: e0228090.

Nieto, S., P. Flombaum, and M. F. Garbulsky. 2015. "Can Temporal and Spatial NDVI Predict Regional Bird-Species Richness?" *Global Ecology and Conservation* 3: 729–35.

Oindo, B. O., and A. K. Skidmore. 2002. "Interannual Variability of NDVI and Species Richness in Kenya." *International Journal of Remote Sensing* 23: 285–98.

Palmer, M. W. 1995. "How Should One Count Species?" *Natural Areas Journal* 15: 124–35.

Palmer, M. W., P. G. Earls, B. W. Hoagland, P. S. White, and T. Wohlgemuth. 2002. "Quantitative Tools for Perfecting Species Lists." *Page Environmetrics* 13: 121–37.

Pearman, P. B., S. Lavergne, C. Roquet, R. Wüest, W. Zimmermann, and N. E. Thuiller. 2014. "Phylogenetic Patterns of Climatic, Habitat and Trophic Niches in a European Avian Assemblage." *Global Ecology and Biogeography* 23: 414–24.

Peckham, S. D., D. E. Ahl, S. P. Serbin, and S. T. Gower. 2008. "Fire-Induced Changes in Green-Up and Leaf Maturity of the Canadian Boreal Forest." *Remote Sensing of Environment* 112: 3594–603.

Petchey, O. L., and K. J. Gaston. 2006. "Functional Diversity: Back to Basics and Looking Forward." *Ecology Letters* 9: 741–58.

Pettorelli, N. 2013. *The Normalized Difference Vegetation Index.* Oxford: Oxford University.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. "The Normalized Difference Vegetation Index (NDVI): Unforeseen Successes in Animal Ecology." *Climate Research* 46: 15–27.

Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. "Using the Satellite-Derived NDVI to Assess Ecological Responses to Environmental Change." *Trends Ecology Evolutio* 20: 503–10.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, R. C. Team, and R Core Team. 2019. "Nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-140."

Price, B., C. A. McAlpine, A. S. Kutt, D. Ward, S. R. Phinn, and J. A. Ludwig. 2013. "Disentangling how Landscape Spatial and Temporal Heterogeneity Affects Savanna Birds." *PLoS One* 8: e74333.

Qiao, K., W. Zhu, Z. Xie, and P. Li. 2019. "Estimating the Seasonal Dynamics of the Leaf Area Index Using Piecewise LAI-VI Relationships Based on Phenophases." *Remote Sensing* 11: 2–16.

R Development Core Team, R. 2019. *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing.

Redding, D. W., K. Hartmann, A. Mimoto, D. Bokal, M. DeVos, and A. Mooers. 2008. "Evolutionarily Distinctive Species Often Capture more Phylogenetic Diversity than Expected." *Journal of Theoretical Biology* 251: 606–15.

Regos, A., L. Tapia, S. Arenas-Castro, A. Gil-Carrera, and J. Domínguez. 2021. "Ecosystem Functioning Influences Species Fitness at Upper Trophic Levels." *Ecosystems* 25: 1037–51.

Rocchini, D., N. Balkenhol, G. A. Carter, G. M. Foody, T. W. Gillespie, K. S. He, S. Kark, et al. 2010. "Remotely Sensed Spectral Heterogeneity as a Proxy of Species Diversity: Recent Advances and Open Challenges." *Ecological Informatics* 5: 318–29.

Rocchini, D., D. S. Boyd, J. B. Féret, G. M. Foody, K. S. He, A. Lausch, H. Nagendra, M. Wegmann, and N. Pettorelli. 2016. "Satellite Remote Sensing to Monitor Species Diversity: Potential and Pitfalls." *Remote Sensing in Ecology and Conservation* 2: 25–36.

Salvatore Mangiafico. 2021. "rcompanion: Functions to Support Extension Education Program Evaluation. R package version 2.4.1."

Semeraro, T., G. Vacchiano, R. Aretano, and D. Ascoli. 2019. "Application of Vegetation Index Time Series to Value Fire Effect on Primary Production in a Southern European Rare Wetland." *Ecological Engineering* 134: 9–17.

Seto, K. C., E. Fleishman, J. P. Fay, and C. J. Betrus. 2004. "Linking Spatial Patterns of Bird and Butterfly Species Richness with Landsat TM Derived NDVI." *International Journal of Remote Sensing* 25: 4309–24.

Sklenicka, P. 2016. "Classification of Farmland Ownership Fragmentation as a Cause of Land Degradation: A Review on Typology, Consequences, and Remedies." *Land Use Policy* 57: 694–701.

Sol, D., C. González-Lagos, D. Moreira, J. Maspons, and O. Lapiedra. 2014. "Urbanisation Tolerance and the Loss of Avian Diversity." *Ecology Letters* 17: 942–50.

Son, N. T., C. F. Chen, C. R. Chen, V. Q. Minh, and N. H. Trung. 2014. "A Comparative Analysis of Multitemporal MODIS EVI and NDVI Data for Large-Scale Rice Yield Estimation." *Agricultural and Forest Meteorology* 197: 52–64.

Soudani, K., C. François, G. le Maire, V. le Dantec, and E. Dufrêne. 2006. "Comparative Analysis of IKONOS, SPOT, and ETM+ Data for Leaf Area Index Estimation in Temperate Coniferous and Deciduous Forest Stands." *Remote Sensing of Environment* 102: 161–75.

Souza, F. L., F. Valente-Neto, F. Severo-Neto, B. Bueno, J. M. Ochoa-Quintero, R. R. Laps, F. Bolzan, and F. de Oliveira Roque. 2019. "Impervious Surface and Heterogeneity Are Opposite Drivers to Maintain Bird Richness in a Cerrado City." *Landscape and Urban Planning* 192: 103643.

Stagoll, K., D. B. Lindenmayer, E. Knight, J. Fischer, and A. D. Manning. 2012. "Large Trees Are Keystone Structures in Urban Parks." *Conservation Letters* 5: 115–22.

Stein, A., K. Gerstner, and H. Kreft. 2014. "Environmental Heterogeneity as a Universal Driver of Species Richness across Taxa, Biomes and Spatial Scales." *Ecology Letters* 17: 866–80.

St-Louis, V., A. M. Pidgeon, M. K. Clayton, B. A. Locke, D. Bash, and V. C. Radeloff. 2009. "Satellite Image Texture and a Vegetation Index Predict Avian Biodiversity in the Chihuahuan Desert of New Mexico." *Ecography* 32: 468–80.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, F. Jeltsch, et al. 2004. "Animal Species Diversity Driven by Habitat Heterogeneity/Diversity: The Importance of Keystone Structures." *Journal of Biogeography* 31: 79–92.

Tucker, C. J. 1979. "Red and Photographic Infrared Linear Combinations for Monitoring Vegetation." *Remote Sensing of Environment* 8: 127–50.

Tucker, C. M., and M. W. Cadotte. 2013. "Unifying Measures of Biodiversity: Understanding when Richness and Phylogenetic Diversity Should be Congruent." *Diversity and Distributions* 19: 845–54.

Tucker, C. M., M. W. Cadotte, S. B. Carvalho, T. J. Davies, S. Ferrier, S. A. Fritz, R. Grenyer, et al. 2016. "A Guide to Phylogenetic Metrics for Conservation, Community Ecology and Macroecology." *Biological Reviews* 92: 698–715.

Turner, D. P., W. D. Ritts, W. B. Cohen, T. K. Maeirsperger, S. T. Gower, A. A. Kirschbaum, S. W. Running, et al. 2005. "Site-Level Evaluation of Satellite-Based Global Terrestrial Gross Primary Production and Net Primary Production Monitoring." *Global Change Biology* 11: 666–84.

Turner, W., E. J. Sterling, and A. C. Janetos. 2001. "Contributions of Remote Sensing to Biodiversity Conservation: A NASA Approach." *Conservation Biology* 15: 832–4.

United Nations. 2017. "New Urban Agenda."

United Nations Human Settlements Programme. 2022. *World Cities Report 2022: Envisaging the Future of Cities*. Nairobi: United Nations.

Venables, W. N., and B. D. B. Ripley. 2002. *Modern Applied Statistics with S*, Fourth ed. New York: Springer.

Vermote, E. 2013. "Climate Algorithm Theoretical Basis Document (C-ATBD): AVHRR Land Bundle-Surface Reflectance and Normalized Difference Vegetation Index."

Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. "New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology." *Ecology* 89: 2290–301.

Wang, Q., S. Adiku, J. Tenhunen, and A. Granier. 2005. "On the Relationship of NDVI with Leaf Area Index in a Deciduous Forest Site." *Remote Sensing of Environment* 94: 244–55.

Waring, R. H., N. C. Coops, W. Fan, and J. M. Nightingale. 2006. "MODIS Enhanced Vegetation Index Predicts Tree Species

Richness across Forested Ecoregions in the Contiguous USA." *Remote Sensing of Environment* 103: 218–26.

Waser, L. T., S. Stofer, M. Schwarz, M. Küchler, E. Ivits, and C. Scheidegger. 2004. "Prediction of Biodiversity - Regression of Lichen Species Richness on Remote Sensing Data." *Community Ecology* 5: 121–33.

Webb, C. T. 2010. "A Structured and Dynamic Framework to Advance Traits-Based Theory and Prediction in Ecology." *Ecology Letters* 13: 267–83.

Williams, N. S. G., M. W. Schwartz, P. A. Vesk, M. A. McCarthy, A. K. Hahs, S. E. Clemants, R. T. Corlett, et al. 2009. "A Conceptual Framework for Predicting the Effects of Urban Environments on Floras." *Journal of Ecology* 97: 4–9.

Wright, D. H. 1983. "Species-Energy Theory: An Extension of Species-Area Theory." *Oikos* 41: 496–506.

Wright, K. 2018. "Corrgram: Plot a Correlogram. R package version 1.13."

Wu, X., H. Xu, and Q. Jiang. 2020. "Cross-Comparison of GF-1, GF-2 and Landsat-8 OLI Sensor Data." *Wuhan Daxue Xuebao (Xinxi Kexue Ban)/Geomatics and Information Science of Wuhan University* 45: 20190084.

Wu, Y., R. K. Colwell, C. Rahbek, C. Zhang, Q. Quan, C. Wang, and F. Lei. 2013. "Explaining the Species Richness of Birds along a Subtropical Elevational Gradient in the Hengduan Mountains." *Journal of Biogeography* 40: 2310–23.

Xue, J., and B. Su. 2017. "Significant Remote Sensing Vegetation Indices: A Review of Developments and Applications." *Journal of Sensors* 2017: 1–17.

Zhao, J., J. Li, Q. Liu, H. Wang, C. Chen, B. Xu, and S. Wu. 2018. "Comparative Analysis of Chinese HJ-1 CCD, GF-1 WFV and ZY-3 MUX Sensor Data for Leaf Area Index Estimations for Maize." *Remote Sensing* 10: 68.

Zhengxing, W., L. Chuang, and H. Alfredo. 2003. "From AVHRR-NDVI to MODIS-EVI: Advances in Vegetation Index Research." *Acta Ecologica Sinica* 23: 979–87.

Zoological Society of London. 2008. "Edge of Existence Programme." http://www.edgeofexistence.org.

Zupan, L., M. Cabeza, L. Maiorano, C. Roquet, V. Devictor, S. Lavergne, D. Mouillot, N. Mouquet, J. Renaud, and W. Thuiller. 2014. "Spatial Mismatch of Phylogenetic Diversity across Three Vertebrate Groups and Protected Areas in Europe." *Diversity and Distributions* 20: 674–85.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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