Faculty of
Environmental Sciences

Applying different methods for bird conservation across European countries

Doctoral thesis (*compilation of published works*)

Ing. Kristina Cerman

Czech University of Life Sciences, Faculty of Environmental Sciences

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Ph.D. candidate: Kristina Cerman

Programme: Applied and Landscape Ecology

Department: Department of Ecology

Advisor: doc. Federico Morelli

Consultant: Yanina Benedetti, Ph.D.

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Declaration

I declare that this Ph.D. thesis is my original authorial work under the supervision of Federico Morelli, PhD, which I have written on my own, except co-authors contributions to enclosed papers and manuscripts. This thesis or its parts were not submitted to obtain any other or the same academic title.

Prague, 2023 ……………………….

Annotation

This study investigates the different methods that can be applied to contribute species conservation. Study covered 11 European countries, Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Czechia, Greece, Montenegro, North Macedonia, Serbia, Slovenia, and Spain. Study analysed the effectiveness of protected areas in conserving temporal changes of bird species richness in Czechia; effectiveness of conserving different bird diversity components (taxonomic, functional and phylogenetic diversity) in Spanish protected areas; performed spatial distribution models (SDMs) of two endangered owl species in the Balkan Peninsula, covering 9 countries (Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Greece, Montenegro, North Macedonia, Serbia, and Slovenia) in the face of climate change; and quantified niche overlap and spatial distribution of five *Columbidae* species in different landscapes. In general, results showed that protected areas are effective in mitigating landscape changes and maintaining species richness, as well as covering different bird diversity components. Results were not as positive when it came to studying two endangered owl species, when it was revealed that their spatial distribution will shrink as a response to climate change. Finally, quantification of niche overlap showed there was intraspecific competition between five *Columbidae* species and that their overlap was mainly in urban areas. Main conclusion from applying different methods showed that each method had its limitations and strengths, however majority of the methods we applied had conservation implications and contributed to filling knowledge gaps in certain topics. Furthermore, our results provided valuable information for future conservation plans in these countries.

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1. Literature review

1.1. Introduction

With the current biodiversity decline in the World due to different adverse effects of human impacts, the need for studying species conservation and applying different methods is growing. Conservationists are fighting numerous threats to species, to name a few: illegal wildlife trade, habitat loss, the spread of invasive species, etc. Along with fighting against these threats, they are setting up programs for species protection and reintroduction, habitat restoration, and implementation of legal protection within protected areas. These are all only some conservation methods that contribute to the mitigation of species threats. Different areas of the World are facing different challenges in species conservation. Hence, providing more detailed information on a continental and national level about which species are threatened and what mitigation techniques might be beneficial for conservation efforts.

According to a recent report, 39% of bird species in the EU are in poor and bad conservation status, which means that some negative human impacts threaten the species. The most threatened species at the EU level are (BirdLife International, 2022):

- waterbird species due to habitat loss and pollution,
- raptor species due to the high roadkill mortality rate, and
- farmland birds due to agricultural intensification.

Still, the previously mentioned threats to species are on the continental level, and conservation challenges would differ nationally. However, sometimes more detailed information about these challenges is not available, and additional research is needed to provide a better understanding of conservation needs. Therefore, my thesis studied different ways to humbly contribute to filling knowledge gaps in European species conservation.

During the four years of my research, I worked on several different topics in bird species conservation. In my research, I applied different methods that have conservation implications and have provided significant results. My published research contributes to knowledge of the advantages and disadvantages of several methods applied when studying bird species conservation.

The following literature review will cover the main topics related to my research. Starting from introducing biodiversity as a term, its importance, and threats. Understanding the background of biodiversity is an essential asset in conservation, as well as how to measure biodiversity, the so-called biodiversity metrics or indices, their importance in species conservation, and how they are applied. Furthermore, I will look into the bird population trends and their drivers on a European and local scale in different European countries. After introducing biodiversity terms, its threats and how to measure them, and species trends in the face of these threats, I will introduce one of the oldest conservation methods – protected areas. Then cover the importance of protected areas, their contribution to species conservation in the face of adverse human impacts, and if the protected areas are efficient in protecting different aspects of biodiversity. The next chapter will cover species distribution models (SDMs) as one of the modern species conservation methods that have been rising in the past two decades due to their potential to predict species distribution in future climatic conditions. And finally, investigate the niche overlap among similar species as an important tool in species conservation.

I aspired to cover and cite the newest and most relevant studies published on the topics mentioned above to present to the readers the current state of the art of bird species conservation in Europe. However, I am aware that my thesis does not cover all the essential conservation methods available. Therefore, I hope that with future collaborations I have made during my research, I will continue humbly contributing to the conservation of birds in Europe.

1.2. Aims of the thesis

In this thesis, I studied different bird conservation methods across several European countries. At first, I was interested in studying the efficiency of protected areas in the conservation of bird species in Czechia and in their coverage of different biodiversity aspects in Spain, which I studied for my master's thesis as well. However, as I continued with my research, I also thought about adding other conservation measures to have a clearer picture of what would work best in bird species conservation. Therefore, I applied species distributions models with bird species data from the Balkan peninsula (Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Greece, Montenegro, North Macedonia, Serbia, and Slovenia), Czechia, and Spain (Figure 1).

The specific aims were to assess if:

(i) protected areas in Spain contributed to the protection of different aspects of biodiversity (Morelli et al., 2021);
(ii) analyse temporal changes of bird communities inside and outside protected areas in Czechia (Floigl et al., 2022b);
(iii) develop SDMs for two endangered species and try to predict their future distributions in the face of climate change in the Balkan peninsula (Cerman et al., 2022);
(iv) and finally quantify the habitat overlap of five closely related species in Czechia (Floigl et al., 2022a).

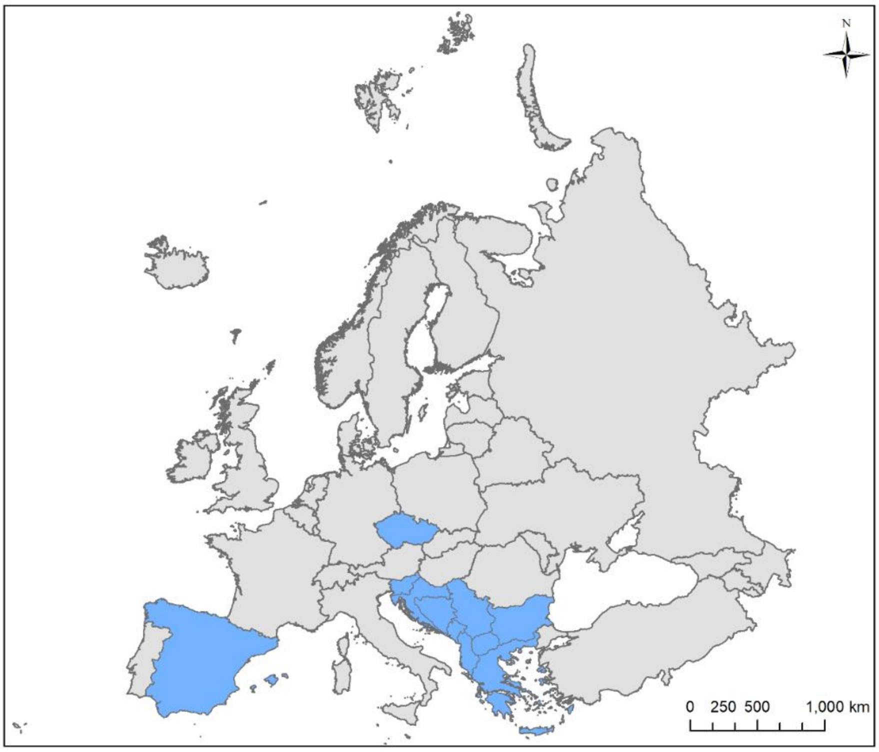

Figure 1. In blue colour are study areas of separate manuscripts published for the purpose of my thesis entitled "Applying different methods for bird conservation across European countries ". Bird species and environmental data was obtained from Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Czechia, Greece, Montenegro, North Macedonia, Serbia, Slovenia, and Spain.

1.3. Literature review

1.3.1. Biodiversity – definition, importance, and its threats

Biodiversity conservation is a cornerstone of nature conservation. The Convention on Biological Diversity (CBD) defined *biodiversity* as "the variability among living organisms from all sources including, among other things, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.". Biodiversity is a fundamental component of planet life-support systems, and humans' well-being depends on nature's services, such as essential material goods, underpinning functions, and non-material benefits (Mace et al., 2011; MEA – Millennium Ecosystem Assessment, 2005; Rands et al., 2010). Term "biological diversity" traces back to early 1950's, however the more widely used term "biodiversity" was coined 30 years later by Walter G. Rosen (Magurran, 2004). Even though numerous reports, studies, and assessments have been published to raise awareness, biodiversity on our planet has been declining at an alarming rate in recent decades. Considerable evidence suggests that we are facing a sixth mass extinction event called Holocene or Anthropocene extinction (Cowie et al., 2022; IPBES, 2019). The name Anthropocene extinction comes from the fact that it is primarily driven by human activities such as agricultural expansion, industrial development, and rapid increase in the human population (Ceballos et al., 2015).

There are several important conventions related to the conservation of biodiversity, such as the beforehand mentioned Convention on Biodiversity (CBD), the Ramsar Convention on Wetlands, the Bern Convention - The Convention on the Conservation of European Wildlife and Natural Habitats, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). As well as many international and national nature conservation legal acts and directives, such as the Birds and Habitat Directives (European Commision, 1992; European Commission, 2009) in the European Union (EU). However, in spite of all conventions, legal directives and laws set in plate the current rate of extinction is exceptionally high, it is calculated to be 100 to 1,000 times bigger than natural background extinction rates (Pimm et al., 2014). Furthermore, this rate is predicted to continue increasing in the forthcoming decades (Ceballos et al., 2015). In light of this, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) has recognised five critical drivers of biodiversity loss and species extinction. These drivers are habitat loss, invasive alien species, overexploitation of natural resources, environmental pollution, and global climate change (IPBES, 2019). Therefore, to reduce the impact of the mentioned drivers of biodiversity loss, conservationists had to come up with several methodologies to measure biodiversity to apply proper conservation measures.

1.3.2. Biodiversity metrics

Scientists have come a long way in studying different types of biodiversity metrics and currently there are three main attributes that biodiversity encompasses: taxonomic (Magurran, 2004), functional (Mouchet et al., 2010), and phylogenetic diversity (Faith, 1992). Each of these metrics focuses on a different attribute of biodiversity and provides a different insight into species communities and what processes are occurring.

Taxonomic diversity proposes that all species and individuals are equal in the ecosystem, therefore it does not look at functional and evolutionary differences between species in a community (Devictor et al. 2010). It includes metrics such as species richness and abundance of species. Species richness is the number of species in the unit of study, whereas abundance of species is number of individuals of each species in the unit of study (Magurran, 2004). Nevertheless, species richness is at focus when calculating taxonomic diversity because it represents the presence of species in a community (Lee and Martin 2017). Therefore, species richness is vastly used with different approaches, methodologies, and focus species. For instance, in studies assessing effectiveness of protected areas in species conservation (Floigl et al., 2022b; Morelli et al., 2021; O'Dea et al., 2006), studies assessing effects of different biodiversity loss drivers (Reif et al., 2013; Verhulst et al., 2004; Zhang et al., 2013), or studies investigating species' habitat distribution and ecological niche (Floigl et al., 2022a; Solhjouy-Fard and Sarafrazi, 2016). On the other hand, disadvantage of taxonomic diversity is that it fails to account for species traits and phylogenetic lineage, which excludes species ecological role in communities (Safi et al., 2013). Therefore, functional diversity is recognised as a more important biodiversity metric by conservationists.

Functional diversity is species-trait based and are used for assessing the diversity of communities (de Bello et al., 2010; Flynn et al., 2011). Furthermore, functional diversity can recognise variation in ecosystem function, processes underlying species communities and relationships occurring in the ecosystem which is beyond the scope of taxonomic diversity. The use of the term “functional diversity” in studies has increased since the beginning of the 21st century and has been used for a wide range of taxa, including bacteria, invertebrates and vertebrates (Petchey and Gaston, 2006). There are several definitions explaining this complex term, however the widely accepted definition is the “value and the range of species and organismal traits that influence ecosystem functioning” (Tilman, 2001). Even though there are several definitions, all have one common point that functional diversity always considers organisms as “dynamic entities that interact with their environment” (Calow, 1987). However, even though it can provide a more complex insight into species communities it is considered to be a difficult term to interpret in research studies due to its complex nature (Petchey and Gaston, 2006). Regarding application of functional diversity metrics in ecological studies, here are some of the commonly used ones (Morelli et al., 2018b):

- Functional diversity – diversity calculated using avian niche traits (Petchey and Gaston, 2006);
- Functional dispersion - the mean distance in the multidimensional trait space of individual species to the centroid of all species in the community (Mason et al., 2013);
- Functional richness – the amount of functional space occupied by a species assemblage (Mason et al., 2005);
- Functional evenness – indicate how regular is the degree to which the biomass of the species assemblage is distributed in the niche to allow effective use of the entire range of resources available (Mason et al., 2005);
- Functional divergence – how far are high species abundances from the centre of the functional space (Mason et al., 2005);
- Rao’s quadratic entropy (RaoQ) – the sum of pairwise distances

between species weighted by relative abundance (Botta-Dukát, 2005).

Moreover, application of species traits in studies has been widely used in species conservation to understand the effects of environmental conditions on species communities (Devictor and Robert, 2009). Although grouping species according to their functional traits as a faster method has been proved to be inferior to the functional diversity indices, researchers still widely use it in combination with functional diversity indices (Mason et al., 2005). The method consists of assigning each species to a functional trait group based on the life-history attributes, it goes without saying that chosen species traits will depend on taxa, study aim, research question, and methodology. For instance, in research focusing on bird species conservation, species traits most used are habitat specialisation, mobility, body mass, nest type, nest location, and diet (Morelli et al., 2021; Rayner et al., 2014; Reif and Flousek, 2012). Furthermore, importance of functional diversity measures is mirrored in their ability to reflect underlying processes in species assemblages such as biotic homogenisation, when only a few species are present (Devictor et al., 2010; Morelli et al., 2016).

Phylogenetic diversity is an essential component of macroecology, community ecology and conservation biology (Faith, 1992). It refers to differences in phenotypes, genetic characteristics and behaviour between species that belong to different evolutionary lineages. It is hypothesised that closely related species are more functionally similar than distantly related species, hence the more distantly related species in a community, i.e., more phylogenetically diverse community, will be more functionally complex (Thompson et al., 2015). Regarding application of phylogenetic diversity indices in studies, it is usually used as complementary index to species richness since conservationists consider that loss of evolutionary diversity plays a great role in global extinction rates. In the past two decades there has been an increased application of phylogenetic indices in conservation biology including various taxa, e.g., birds (Jetz et al., 2014; Jiguet et al., 2012; Meynard et al., 2011; Morelli et al., 2021), plants (Pollock et al., 2015; Zhang et al., 2015). Some of the most used phylogenetic diversity indices are:

- Evolutionary distinctiveness – an important tool used in identifying species and communities which have higher values in terms of evolutionary heritage. The index is estimated using the sum of the branch lengths of all species present in an assemblage (Morelli et al., 2018b);

- Community evolutionary distinctiveness – a measure of species uniqueness, calculated as mean evolutionary distinctiveness for each community (Morelli et al., 2016; Tucker et al., 2017);
- Phylogenetic diversity – a sum of all lengths of all branches in a defined phylogenetic tree (Jetz et al., 2014).

1.3.3. Bird population trends and their drivers across several European countries

A detailed study looking into different groups of bird species, showed that in the period from 1980 – 2015 bird abundance in Europe declined by 17%– 19% (Burns et al., 2021). The same study showed that more than 25% of agricultural bird species populations declined within the same period. Since almost 40% of the EU’s land area is covered by agricultural lands (Eurostat, 2022), it is expected that main driver of biodiversity loss is agriculture. A lot of research focus has been on the decline of farmland species in the past 20 years and understanding the background processes (e.g., Donald et al., 2001; Reif and Hanzelka, 2020; Schmidt et al., 2022). Furthermore, wetland and migratory bird species are declining due, both due to habitat loss (Mao et al., 2019). On the other hand, urban species populations have been increasing since there are less predators in urban areas than in more natural landscapes.

However, when looking at a local level of species decline other drivers are present too. Since, my research was conducted in the Balkan region, Czechia, and Spain these are the countries I will discuss in more details. Although these countries all have one common driver – agricultural intensification, there are some that are characteristic for local areas. Due to the geopolitical situation in Europe over the past decades, Western Europe is facing higher agricultural intensification and land homogenization because of earlier development of countries and entrance to the EU (Báldi and Batáry, 2011). On the other hand, Eastern and Southern Europe are faced with different challenges, such as land abandonment and fragmentation of land ownership due to longer periods of communistic regime in these areas, followed by later entrance to the EU (Sutcliffe et al., 2015). Therefore, different management techniques are suggested when it comes to endangered farmland species, in the Western Europe to introduce more management techniques of degraded agricultural habitats and in Southern Europe prevent intensification of agriculture (Reif and Hanzelka, 2020).

For instance, looking at the Balkan region mountain specialists are endangered by the development of ski resorts which causes habitat fragmentation and destruction (Rajković et al., 2010; Shurulinkov et al., 2007). Furthermore, not the entire Balkan region is in the EU (Albania, Bosnia and Herzegovina, North Macedonia, and Serbia are not) therefore Natura 2000 network does not cover endangered habitats in these countries which only depend on the network of national protected areas. Unfortunately, national protected areas often fail to meet conservation measures and species protection. Additionally, in the Balkan region there is insufficient research in bird population trends and species protection (Puzović et al., 2015). However, in Czechia and Spain there are various research on bird populations trends and species protection. Looking at Czechia, there is a different driver of forest specialists decline recorded in the past 10 years – invasive species, bark beetle (*Ips typographus*, Linnaeus 1758), which have led to forest disturbances (Fiala et al., 2019; Sarbu et al., 2014). Finally, looking at Spain major driver of species loss is the agricultural industry; however, it’s related mostly to loss of habitat, such as steppes, fallow lands and marginal vegetation as a key habitat for several farmland specialists (Traba and Morales, 2019).

1.3.4. Species conservation methods

There are various species conservation methods, and it is not possible to pinpoint to the most efficient one. However, ecologists suggest that combination of different methods is the key to successful species conservation. Just to name a few most efficient ones:

1. Habitat protection – mostly done by designation of protected areas for specific types of habitats. For instance, wetlands are one of the most endangered habitat

type in Europe and are therefore protected by Ramsar Convention (Mauerhofer et al., 2015).

2. Legal regulations – as described above there are multiple international conventions dealing with the protection of biodiversity, however legal regulations on a national level differ and can help save local species populations. For example, introduction of hunting bans during breeding and migratory seasons, or a complete ban of species hunting.
3. Education and citizen science: help raise awareness of locals by educating them on the importance of species protection, as well as encouraging them to contribute by providing data can be beneficial for the research purposes.
4. Species monitoring and research – population and environmental monitoring is essential in species conservation to help gain insight where conservation measures are necessary.

Although the above-mentioned conservation methods are the most common ones which ecologist and conservationists are applying, there are other methods that are simpler and contribute to these general ones by providing new relevant insights on species distributions, their behaviour, and current population trends.

After listing species trends, their main drivers of decline, it is evident species conservation is of far most importance in the 21st century. Therefore, applying different methods of species conservation such as designating protected areas for better coverage of endangered species and their habitats, applying species distribution models (SDMs) to find out current and future geographic distribution of endangered species in the face of climate change, and understanding species ecological niche. These are just some of the methods that provide humble contributions to future research of species conservation.

1.3.5. History of protected areas and their modern heritage

Desire to protect nature has been around since 300 BC, when Indian emperors established protected areas for elephants and forests, which was followed by protection of other areas as hunting grounds. However, it wasn’t until 1872 that a first modern protected area, as we know them today, was established in the United States – the Yellowstone National Park (Chape et al., 2009). This trend followed on other continents as well, as first modern protected areas were designated, El Chico National Park in Mexico, South America; Angkor Wat in Cambodia, Asia; Kruger National Park in Africa; and the Swiss National Park in Switzerland, followed by Bialowieza Forest in Poland, in Europe. Although these early modern protected areas did not have the same conservation goals and management strategies as they have today, their establishment was one of the first key steps to modern nature conservation.

Historically, focus for designation of protected areas was slightly different than today. There was a trend of protecting and focusing on hotspots of biodiversity and this was one of the main pillars of nature conservation (Lascelles et al., 2012). Therefore, areas with the greatest number of species would receive highest protection and most attention. Such hotspots of species richness, endemism, and areas with species taxonomically unique for the area is one of the approaches that is used on an international level. Hotspots of biodiversity are identified as areas with high species endemism and habitat loss (Myers et al., 2000). To this day list of global biodiversity hotspots contains 36 areas, the last one to be added was North American Coastal Plain in 2016 (International Conservation, 2022). Biodiversity hotspots have been identified by Myers in a paper published in 2000 and later it was revised by Mittermeier et al. (2004) and Sloan et al. (2014). These areas cover merely 2.5 % of Earth’s surface. Criterion to make the list of biodiversity hotspots are (i) area has to include at least 1,500 vascular endemic plants and (ii) have 30% or less than its original vegetation cover i.e., be threatened (Myers et al., 2000). These strict criteria have been used till today to add more areas to the list of hotspots (Sloan et al., 2014). Although the hotspots are protecting large areas and are inhabited by many endangered species, this type of protection is only a small friction of protected areas around the World.

There are many classifications of protected areas according to their level of protection, size, and accessibility to the public. Therefore, I will not cover all types of protected areas here but discuss the most important classifications and the ones that were used in my research. One of the most famous international classifications of protected areas is the one provided by the International Union for Conservation of Nature (IUCN). A clear definition of protected areas provided by the IUCN states that “A protected area is a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (IUCN, 2022). The IUCN recognises seven categories, each with a different management objective and level of protection: (Ia) Strict Nature Reserve, (Ib) Wilderness Area, (II) National Park, (III) Natural Monument, (IV) Habitat/Species Management Area, (V) Protected Landscape, (VI) Protected area with sustainable use of natural resources (IUCN, 2022). Although some of these names of categories overlap with the names of categories of protected areas designated on the national level, they are not to be confused with one another, since often these categories will have different levels of protection.

Since my research was conducted only in European countries, I am going to introduce here in more depth the European Union’s (EU) protected area network, Natura 2000. This transnational network protects both endangered species and their habitats, and it encompasses two directives: Birds and Habitat Directives adopted in 1979 and 1992, respectively. Each directive designates different types of protected areas which in many cases overlap partially or fully. Sites of Community Interest (SCIs) protect 233 habitat types and 900 species that are listed on the Annex II of the Habitat Directive (European Commision, 1992). These sites must be managed according to the species’ ecological needs. Furthermore, Special Protection Areas (SPAs) designated according to the Birds Directive are designed to protect 193 endangered bird species listed in Annex I of the Birds Directive and the migratory species (European Commission, 2009). With currently covering over 18% of the EU’s land, Natura 2000 network is the largest network of protected areas in the world (European Environment Agency, 2019a). Moreover, the importance of Natura 2000 is mirrored in its transnational essence to overlap with the national protected areas. Consequently, endangered species and their habitats will benefit from the physical protection of individuals and conservation of core breeding and resting sites due to the requirements of the Birds and Habitat Directives (European Environment Agency, 2019b). It’s been proved that the national and international legislations play an important role in providing species the necessary protection (Koschová et al., 2018).

Therefore, effective protected areas are a crucial conservation measurement in Europe for the protection of habitats and species. Due to the negative effects of agriculture (Reif and Hanzelka, 2020; Traba and Morales, 2019), land-use changes

(Gaüzère et al., 2020), climate changes (A. Lehikoinen et al., 2019) and other drivers European bird populations have been in decline (Burns et al., 2021; Frenzel et al., 2016). For instance, mountain specialists in Europe have declined by 10% in species populations numbers in the period of 2002-2014 and the trend continues (A. Lehikoinen et al., 2019). To be able to conserve bird species in protected areas, monitoring land-use changes, species richness, and any changes subjected to time, temporal changes, is an essential part of conservation measures. These types of changes can provide more insight into species populations and benefit species protection (Koleček et al., 2010). Hence, the urgent need to monitor temporal changes of environmental variables inside protected area. Moreover, species conservation benefits from monitoring environmental variables inside protected areas by providing insight into occurring biological processes and informing whether the conservation measures need to be adjusted accordingly (Floigl et al., 2022b). Studies have shown the positive effects of protected areas in increasing populations of endangered species (Donald et al., 2007), protecting species habitats (Devictor et al., 2007), and serving as refugia to species in the face of climate change (Gaüzère et al., 2016; P. Lehikoinen et al., 2019; Thomas and Gillingham, 2015). Moreover, research shows - protected areas minimise before mentioned harmful effects on species even for which they were not designated for, this phenomenon is known as “umbrella effect” (Van Der Sluis et al., 2016). Additionally, increase in the abundance of bird species not listed on the Annex I inside Natura 2000 network was reported (Pellissier et al., 2019), suggesting that protected areas provide more stable habitats for species. Besides, protected areas contribute to higher bird species richness by applying conservation and management strategies and providing more stable ecosystems, by protecting habitats (Watson et al., 2014), and by mitigating the negative effects of climate change (Gaüzère et al., 2016).

Additionally, the EU adopted a new Biodiversity Strategy for 2030. The strategy’s objectives are to build resilience to climate change impact, forest fires, food insecurities, and disease outbreaks by fighting illegal wildlife trade by 2030. The strategy contains specific actions to be delivered by 2030, through which the above-mentioned objectives would be achieved. The EU plans to enlarge its protected areas network, Natura 2000, and put the focus on areas with high biodiversity. However, similar strategy has already been proposed before for 2020, and research shows little improvement has been made (Hermoso et al., 2019).

1.3.6. SDM – species distribution models as a species conservation method

Over the last 30 years scientists have been applying mathematical algorithms for predicting species geographic distributions by using presence and absence datasets and environmental predictors within their current range. The most common method are are species distribution models (SDM) (Elith and Leathwick, 2009; Guisan and Zimmermann, 2000). If used environmental predictors are ecologically relevant for the species, for instance using forest density for forest species, and accurate spatial data are combined in an SDM it is possible to obtain more insight into species distribution. However, misuse of environmental predictors and obtained results are not ecologically significant (Elith and Leathwick, 2009). Application of SDMs in species conservation is multifaceted, it is applied to predict species habitat suitability (Zhu et al., 2020), find areas of conservation concern and focus (Arcos et al., 2012), and predict distributions of invasive species (Chapman et al., 2019; Taucare-Ríos et al., 2016).

Furthermore, using future environmental predictors, such as climate data, with current species distribution data it is even possible to predict future species distribution shifts in the face of climate change and see which areas can serve as refugia in the future (Brambilla et al., 2022; Cerman et al., 2022). With climate change recognised as one of the five key drivers of biodiversity loss (IPBES, 2019), using SDMs for predicting future species distributions has been on the rise in the past several years. The method has been applied using data of various taxa - plants (Khan et al., 2022; Wei et al., 2018), mammals (Moghadam, 2019), birds (Meza Mori et al., 2022; Zhang et al., 2019).

SDMs have been widely used due to the easy and open access databases of species (e.g., GBIF, grey literature) and environmental predictors (e.g., Corine Landcover, WorldClim) (Gomes et al., 2018). Moreover, it’s application in research attracted even more scientists when the machine-learning algorithm MaxEnt (Maximum Entropy) was introduced (Phillips et al., 2006). Other SDMs include using RStudio or Geographic Information System (GIS), however due to MaxEnt’s user-friendly nature that does not require coding it has been the most used modelling approach. Besides, this approach requires only presence data, while including the interactions between predictors, and providing satisfactory models (Elith et al., 2006).

However, performance of SDMs is greatly affected by the used data (Araújo et al., 2019). For instance, by sampling bias and low sampling size of species data (Kramer-Schadt et al., 2013) are the most common errors and pitfalls to be aware of. Additionally, when considering environmental variables, type and origin of data (Moudrý et al., 2019), as well as resolution (Wunderlich et al., 2022) should be checked. Due to the dynamic nature of species distribution, specific species ecological traits, and their relationship with the environment SDMs should be used with caution. Furthermore, modelled species should be researched in advance, as well as determined which environmental data is the most relevant for the studied species and should be applied in SDMs.

1.3.7. Quantification of species niche overlap and spatial distribution

Species ecological niche is a complex concept that is multifaceted and reflects species' relationships with the environment, including the biotic and abiotic factors, and is determined by species behavioural adaptions developed throughout species evolution. Each species occupies a certain space in the ecosystem, which includes its physiological and behavioural traits for survival and reproduction, as well as resources it depends on (Colwell and Futuyma, 1971). However, when two evolutionary similar species co-exist in the same habitat, the niche overlap occurs and can lead to interspecific competition for the same resource (Mason et al., 2011). This can have two outcomes, either local extinction of the weaker competitor or occurrence of niche partitioning where species use the same resources but in unique ways (Finke and Snyder, 2008).

For instance, to avoid niche overlap and partitioning, bird species started colonising other unoccupied habitat, such as urban areas starting from the 20th century (Evans et al., 2010). However, urban bird communities are not as high in species richness as other natural habitats might be, because not many species have yet developed and adapted their ecological traits to cities (Callaghan et al., 2020). Species evolution is a time-consuming complex process, and several decades is not enough for closely related species, for instance pigeons, to develop the intraspecific differences and avoid niche overlap (Tobias et al., 2020).

Quantifying niche overlap and studying spatial distribution of species can provide beneficial inputs to species conservation and help ecologists understand better species needs and requirements to protect them. Furthermore, when species overlap in one habitat and the intraspecific competition is not high, by the umbrella effect it is possible to protect both species and increase effectiveness of protected areas (Maslo et al., 2016). Also, studies on niche overlap and utilisation of the same resources provides information for scarce resource management and points out target resources that need additional conservation attention (Hanane and Yassin, 2017).

2. List of published work

The scientific articles published in peer-reviewed journals represent the core of this thesis are listed below. The articles are in the Annexes section.

Annex I. Floigl, K., Benedetti, Y., Reif, J., Voříšek, P., Morelli, F., 2022. Assessing protected area network effectiveness through the temporal change in avian communities' composition. J. Nat. Conserv. 68. https://doi.org/10.1016/j.jnc.2022.126222

Annex II. Morelli, F., Benedetti, Y., Floigl, K., Ibáñez-Álamo, J.D., 2021. How are Natura 2000 protected areas covering different components of avian diversity in Spain? Ecol. Indic. 133, 108452. https://doi.org/10.1016/j.ecolind.2021.108452

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3. Discussion

3.1. Research I

With my supervisors and in cooperation with co-authors from Charles University and Czech Ornithological Society (CSO) we investigated the effectiveness of Czech protected areas in their ability to mitigate ten-year temporal changes in bird communities. Additionally, we analysed ten-year temporal changes in bird communities along different land use types and landscape heterogeneity, and altitude. For the study purposes, we used data from the national Breeding Bird Monitoring Program in Czechia (Janda and Šťastný, 1984) provided to us by the CSO. We calculated the temporal change, from 2005/2006 to 2014/2015, in bird species richness and in Jaccard dissimilarity index. Our hypotheses were that if protected areas are safeguarding bird communities, temporal changes will be lower and bird species richness will be higher inside protected areas.

For analysing the temporal change in bird communities, we calculated two indices:

(i) Change in species richness from 2005/2006 to 2014/2015 (delta bird species richness)
(ii) Jaccard dissimilarity index (dissimilarity) - the compositional dissimilarity of avian assemblages between both periods

For more detailed methodology see Annex 1.

Our results showed that from 2005/2006 to 2014/2015, bird species richness increased inside protected areas and temporal change was lower inside protected areas, therefore our hypotheses were correct. However, lower temporal changes in bird communities inside protected areas was linked to lowlands. Furthermore, dissimilarity was lower in forests and heterogeneous landscapes. Besides, bird species richness was decreased in mixed environments from 2005/2006 to 2014/2015. Also, land-use richness was negatively associated with the dissimilarity of communities.

We can assume that higher bird species richness in 2014/2015 was due to Czechia's entering the EU in 2004. With becoming a member state, Czechia added the EU's conservation directives to the already existing national Act (Anonym, 2004). Our assumption is supported by the fact that ten years after changing the management strategy in protected areas is sufficient amount of time to observe population changes (Pellissier et al., 2019). The EU's goal to design an international protected area network, Natura2000, and account for transboundary bird species ranges and their migrations has shown to be successful (Koschová et al., 2018). For instance, when looking at our results from Spain, highest species richness was recorded in protected areas designated under both Bird and Habitat Directives or where they overlapped (Morelli et al., 2021). Meaning that the legal protection of one directive contributed to the other directive to support higher number of species. In overall, Natura 2000 network provided efficient protection to bird communities. Moreover, with the EU's nature conservation policies, member states have been recording an increase in populations of species listed on Annex I of the EU's Birds Directive in both Western (Donald et al., 2007; Gamero et al., 2017; Sanderson et al., 2016) and Eastern Europe (Koleček et al., 2014). Species listed on Annex I benefit from the established protected areas, which aim to satisfy species' specific nesting, breeding, and feeding needs (Donald et al., 2007).

One of the protected areas main aim is to maintain suitable habitats for specific species needs (Watson et al., 2014), however more detailed studies have shown that protected areas also protect more common species that are not conservation targets (Devictor et al., 2007; Pellissier et al., 2013). On the other hand, mitigating adverse human impacts, such as climate change, protected areas successfully fulfilled in the case of the temperature adapted species (Gaüzère et al., 2016). However, our study did not include species functional traits into the analysis, and we cannot say with certainty which species benefited more from protected areas. But temporal changes were lower and bird species richness higher inside protected areas, showing that they do support bird communities.

Regarding the effects of altitude, studied bird communities were more similar outside protected areas in mountains. This might be due to the disproportionate coverage of protected areas in mountains vs lowlands (Maiorano et al., 2007). The lowlands are mostly utilised for agricultural purposes, and in Czechia they cover almost 13,000 km^2 (Sadlo and Storch, 2000). Agricultural areas are not protected landscapes and they are unstable ecosystem for bird species (Donald et al., 2001).

Therefore, when comparing landscapes in lowlands with mountains, the former are more exploited areas and the difference between protected and unprotected area is more clear (Kleijn et al., 2011). We cannot state with certainty which one of these factors is the main one, but it is highly possible that it’s the combination of several environmental factors and disproportionate coverage of protected areas.

More similar bird communities, i.e., lower temporal changes, in forests may be due to several reasons such as that the forests are evolutionary older habitat than farmlands and provide more stable ecosystems (Morelli et al., 2018a). Moreover, forests have longer management cycles than farmlands, especially compared to annual crops (Bowler et al., 2019). A Pan-European research analysed decline of insectivorous bird populations, proving that insectivorous forest species had more stable populations than the farmland and grassland species (Bowler et al., 2019). Therefore, forests provide more stable environment for species and the populations of European common forest birds since 1980s appear to be stable (Gregory et al., 2019). Furthermore, decrease in bird species richness from 2005/2006 to 2014/2015 in mixed environments could be attributed to loss of specialist species. This might be due to the nature of mixed environments that provide different types of land-use that are not fit for specialists, but rather for generalists. Ecological traits of specialist species makes them occupy narrow niche and utilise specific resources for diet, nesting, or breeding purposes (Clavel et al., 2011; Morelli et al., 2019). Therefore, specialists are considered a conservation target (Gaston et al., 2008) since they are more prone to local extinctions due to environmental disturbances such as habitat loss, temperature changes, loss of resources etc., (Devictor et al., 2008). Moreover, several studies have reported bird community homogenisation on a continent-wide scale. Community homogenisation is a process of decrease in abundance of species traits (functional diversity), genetic and taxonomic diversity (Olden and Rooney, 2006). The process increasingly received attention in biodiversity conservation since abundance of species traits is one of the key parts of ecosystem services (Devictor et al., 2008; Morelli et al., 2019). Community homogenisation is already reported in Czechia, meaning that some local species extinctions already occurred. For instance farmland specialist *Otis tarda* has disappeared from Czech farmlands (Koleček et al., 2010; Reif et al., 2013). However, out study did not focus on species traits level, but rather on community level, and we cannot confirm this we certainty.

Moreover, low temporal changes in highly heterogenous landscapes was expected since the complex landscape arrangement positively influences bird diversity, confirmed by Tews et al. (2004) in the extensive literature review. Furthermore, published research presented bird species richness to be highly associated with landscape heterogeneity, but not with land-use richness. This might be due to the fact that high species richness will be in heterogeneous landscapes, but if the landscape consists of one land-use type the species richness will be lower (Atauri and De Lucio, 2001). However, our results did not confirm that land-use richness is significant for changes in bird communities. Further investigation of the land-use types might have revealed the reason behind this, but this was not the focus of our study.

To conclude this chapter, the advantage of our study is mirrored in the analysis of data right after implementation of Natura 2000 network in Czechia. Therefore, we could observe the change between the beginning of the implementation of Natura 2000 (2005/2006) and the period ten years after (2014/2015), because ten year interval is enough to see the effects of applied management changes in bird communities (Pellissier et al., 2019). However, out study did not focus separately on national protected areas and Natura 2000 network and therefore we cannot estimate its efficiency, but our results suggest that protected areas in general are safeguarding bird communities. Specifically, mitigating the unfavourable effects of landscape changes on bird communities, such as homogenisation. Finally, the study demonstrates that species richness is supported inside protected areas in Czechia. Although we incorporated some environmental variables, such as land use types, landscape heterogeneity and altitude, other variables such as historical climate data could provide deeper understanding of temporal changes in bird communities.

3.2. Research II

With my supervisor and co-supervisor, we published a manuscript on the coverage of taxonomic (bird species richness), functional and phylogenetic diversity within protected areas in Spain. For the study purposes, we used breeding bird species occurrence obtained from the Spanish Atlas of Breeding Birds (Martí and Del Moral, 2003) and Natura 2000 protected areas boundaries in Spain. Furthermore, we calculated dominant environment for each 10 × 10 km square. As well as bird diversity metrics. For more detailed methodology see Annex 2.

When looking at the taxonomic diversity, results of our research showed that bird species richness is higher inside Natura 2000 network in Spain (Morelli et al., 2021). For the purposes of these study we used Spanish Atlas of Breeding Birds (Martí and Del Moral, 2003). We investigated how protected areas are covering the different components of bird diversity, and study results showed there was a spatial mismatch among three different components of bird diversity. Therefore, when planning and designing protected areas at a large scale it is essential to include this type of research and keep in mind the spatial differences to increase the scope of protection. This is due to the fact that different types of environments support different bird diversity components (Morelli et al., 2018a).

Many studies have already focused on the taxonomic diversity in bird communities and based their conclusions on this simplest component of diversity. However, including other components such as functional diversity can provide better insight into underlying ecological processes within the community. Therefore, we calculated functional dispersion as the measure of functional diversity, to better understand the occurrence of species traits in bird communities. Results reported that mean values of functional dispersion were high inside the Natura 2000 network, meaning that overall, the network was performing well in covering functional diversity of bird communities. However, some gaps in the network's protection were detected. Protected areas designed under Bird Directive did not cover some of the areas where the highest functional dispersion was registered. With the current conservation trends to support species that are evolutionary more unique, with distinct traits, more studies are focusing on the importance of phylogenetic diversity (Gaüzère et al., 2016; Häkkilä et al., 2017). Since disappearance of these species from communities cannot be mitigated by introducing other species. With this in mind, we calculated community evolutionary distinctiveness (CED) as a measure of phylogenetic diversity in bird communities. Our results showed that CED was higher inside both protected areas under Birds and Habitat Directives, which is encouraging for species protection in Spain. Provided results show that Natura 2000 network in Spain is covering and providing beneficial protection to evolutionary unique bird communities. On the other hand, there is research providing opposing results. These results claim that less charismatic species and the ones not listed on Annex I are not benefiting from the legal protection of Natura 2000 network (Rosso et al., 2017; Santana et al., 2014).

Therefore, bird assemblages of specific habitat are not protected, but rather the focus is on flagship species (Caro, 2010).

Our results showed that forests supported higher bird species richness than mixed environments, arable lands, and orchards. This is mainly because forests provide a more stable habitat with less environmental changes than heavily impacted arable lands and have higher habitat complexity, in terms of the vertical structure (Morelli et al., 2018a). In line with our study are results from Italy (Morelli, 2015), and similarly temporal changes in bird species richness was lower in forests in Czechia (Floigl et al., 2022b). Apart from high bird species richness, we also registered high functional dispersion in forests. Although it has been well established that there is a strong positive association between functional diversity and species richness (Petchey and Gaston, 2002), in the study we calculated functional dispersion which is more independent from species richness (Gerisch et al., 2012). Therefore, the spatial congruence is most probably not due to the association with species richness, but due to the type of environment. We can hypothesize that forests foster higher number of species and more ecological species traits. From the point of view of ecologists, high functional dispersion in communities proves there is high functional dissimilarity within the community, making such communities more resilient to environmental changes (Morelli et al., 2021).

Although proven to be useful, biodiversity metrics in species conservation have their limitations. Taxonomic diversity, mainly considering species richness, is limited by only assessing the number of species in a certain area, excluding the abundance and distribution of the species (Fleishman et al., 2006). Hence, omitting the conservation priorities of areas with lower richness, higher populations, and wider distribution of the species. Furthermore, taxonomic diversity does not account for species ecological role in the ecosystem (Morelli et al., 2018a). Meaning that some areas might have high species richness than others, but it does not make them more important from the conservation point of view. For instance, conservation focus on key stone species in the ecosystem is more urgent than other less important species for the ecosystem functioning (Pellissier et al., 2019).

Regarding functional diversity, there are several limitations that should be considered in species conservation studies. Firstly, oversimplification of the species role in ecosystems by limiting the number of functional traits to body size or feeding habits. Followed by species-environment relationship which is complex, and it might not be captured properly just by functional diversity metrics (Laureto et al., 2015). Next limitation is linked to spatial and temporal scales, metrics are usually applied at a single scale which would be misleading since species can vary at different scales. Furthermore, some functional metrics are based on species abundance, which might underestimate the contribution of rare species to ecosystem functioning (Petchey and Gaston, 2002) (Le Bagousse-Pinguet et al., 2019).

In conclusion, results of our research point to the fact that species within protected areas benefit from the legal protection. As well as, that biodiversity components are well covered within protected areas. Furthermore, our research showed that land-use type played an important role in protected area coverage of bird diversity components. This is something that should be considered when implementing our results into species conservation and designing protected areas. As any other research, ours also had certain limitations. We focused on breeding birds only but failed to consider the wintering and migratory species which use protected areas as well during winter and migrations. Future research should consider this aspect of protected areas as well.

3.3. Research III

Since the Balkan Peninsula has been poorly researched and specially in species conservation there are large knowledge gaps, our manuscript provided the first look at current and future species distribution of these two owl species in the entire Balkan Peninsula. Besides, our study provides insight into potential refugia and species area changes along the environmental variables and climate change in the Balkan Peninsula.

In this study, we used the MaxEnt modelling approach, with species data from scientific and grey literature, online database, and records from targeted field surveys using GPS devices. Besides species presence data, we used 19 different bioclimate variables from Global Climate Data–WorldClim version 2.1 (WorldClim, 2022). Also, we used digital elevation model (DEM), slope, aspect, hill shade and soil type in the initial model. Furthermore, to analyse the future spatial distribution in response to climate, we used datasets of future climate predictions from WorldClim. Specifically, Four Shared Socioeconomic Pathways (SSP126, SSP245, SSP370, and SSP585) for two periods 2041-2060 and 2061-2080. For more detailed methodology see Annex 3.

In our paper we applied SDMs to predict potential current species distribution, future species distribution in the face of climate change, and to identify future potential refugia in the Balkan Peninsula for two endangered owl species – Boreal and Eurasian Pygmy Owls. These species are forest predators, depending mostly on coniferous trees in higher altitudes across Europe (Mikkola, 1983). Specifically on the Balkan peninsula, species inhabit mountainous regions with dense forests, and cold climate (Rajković et al., 2013; Shurulinkov et al., 2012), which lowers their tolerance range to climate change (Morelli et al., 2019). About 2% and 3% of Eurasian Pygmy and Boreal Owl, respectively, of European populations is on the Balkan Peninsula (BirdLife International, 2021a, 2016). Furthermore, these two species are listed either as vulnerable or endangered species in all countries from the Balkan peninsula (Rajković et al., 2010; Shurulinkov et al., 2007) making them the perfect fit for applying SDMs.

Our SDMs showed that both species are sensitive to high temperatures, since the variable that contributed the most to spatial distribution was the maximum temperature of the warmest month. However, Boreal Owl was more sensitive to high temperatures than the Eurasian Pygmy Owl which was still present when the temperatures were above 31°C. These results are in line with the previously published study on effects of environmental variable on owl species in Czechia, where Boreal Owl preferred cold temperatures and high elevations (Ševčík et al., 2021). These results are not surprising since Boreal Owl has a circumpolar Holarctic range (Mikkola, 1983), mainly inhabiting northern Europe where they are linked to subalpine coniferous and alpine habitats (Maggini et al., 2014), and southern Europe where they can be found in coniferous forests of Alps (Brambilla et al., 2022), northern Spain (Castro et al., 2008), and the Balkan Peninsula mountain range (Nikolov et al., 2022; Puzović et al., 2015). Following higher temperatures, altitude was the second most influential environmental variable on distribution of Eurasian Pygmy Owl. Although our findings showed that the species prefers high altitudes in the Balkan Peninsula, this might not be the case in the rest of its European range. This is mainly due to the differences in the altitudes of tree lines across Europe, meaning that in the southern species range tree line is in higher altitudes than in the northern species range, since species is a forest specialist and avoids shrubs, grasslands, and open habitats (Ševčík et al., 2021). Moreover, both species showed no significant changes between current and future species distribution in the Balkan Peninsula, meaning that neither species would be able to adapt to new climatic conditions and are therefore limited with high temperatures and low altitudes. In conclusion, both species showed narrow ecological adaptability.

Furthermore, in our study we calculated the potential areas where species would find refuge in the future with warmer climate. The identification of refugia, either where species currently are and could remain in the future or currently unoccupied areas that species could spread to in the future, are a key factor in effective species conservation (Morelli et al., 2020). Additionally, species more sensitive to climate changes, specialist species, are under higher risk of extinction if there is little to no information which areas could potentially be beneficial in the future. Therefore, identifying refugia in advance and considering designating them as protected areas specifically for these species would be a beneficial conservation effort. In the light of this, we calculated refugia based on highly suitable habitat and calculated two types:

- type 1 refugia are habitats where species are present both currently and, in the future, but in different environmental conditions (in situ sites). The most important habitats for species future survival.
- type 2 refugia are habitats that are not suitable in current conditions but provide suitable conditions in all future predictions (ex situ sites).

We followed the methodology proposed by Brambilla et al. (2022).

Our results showed that both type of refugia for the Boreal Owl will be significantly shrinking towards the worst-case climatic scenario, which was expected due to previously discussed species sensitivity to high temperatures. On the other hand, spatial patterns of both types of refugia for the Eurasian Pygmy Owl were not as unified and did not show clear patterns. This might be due to different underlying ecological mechanisms that we did not investigate further within the scope of this study. Although our results were not as clear for the Eurasian Pygmy Owl, including refugia in studies has useful conservation implications. The potential of bird species refugia in the face of climate change has been recognised by many as an important conservation tool (Brambilla et al., 2022; Selwood et al., 2015). Refugia are defined as areas that provide suitable habitats for species to survive and adapt to environmental changes (Stralberg et al., 2015). Since these areas are key targets for conservation planning, and are most likely to preserve ecological conditions for the endangered species (Brambilla et al., 2022). Besides, these refugia would not only be beneficial to particularly these two species that we studied, but to other alpine specialists as well (Brambilla et al., 2022; Morelli et al., 2019). Alpine specialists are the first target of the climate change, since they are limited by high temperatures and if their ecological adaptability is narrow, which is the case of specialists (Morelli et al., 2019), their survival in new conditions is at stake. Climate change may lead to the contraction of suitable habitats for many bird species, and protected areas may not always provide sufficient refugia. It has been proved already that many species will likely shift their ranges poleward or uphill in response to warming temperatures (Flousek et al., 2015; Konvicka et al., 2003; Urbani et al., 2017), and the quality of refugia will be crucial in determining their ability to survive and adapt. To conclude this chapter, future decision-making in species conservation could benefit from our study and use it as a guide which areas should be declared protected areas. These are just some of the positive contributions of SDMs to species conservation.

While SDMs can be useful in avian conservation and predict species distribution in the changing environment, there are certain limitations to it that should be considered when working with them.

First, SDMs are based on the linear relationship between species and the environmental conditions. However, reality is not so black and white. There are several other aspects of species that should be considered, such as history of the distribution, species ecological traits and behaviour, species interactions etc. (Guisan and Zimmermann, 2000). Furthermore, the precision of SDMs will majorly depend on the accuracy and quality of the data used in modelling, and it is important to stress that SDMs could never replace the traditional way of data collection of species distribution, abundance, and interactions (Elith et al., 2006). Finally, SDMs are always predicting for a specific time in the future, such as in our case for two periods 2041-2060 and

2061-2080. Therefore, it is essential to take into consideration the change in species population size (Soriano-Redondo et al., 2019).

To summarise, SDMs should be used with caution and in combination with other conservation tools, which can help understand better species ecological traits, behaviour, and natural underlying background processes. Our study's conservation implications are contributing to the knowledge gap of species distribution of the two owl species, and more importantly providing concrete proof that management of the two species needs to be improved in the future to provide satisfactory conservation results. As well as, pointing out to areas which need to be prioritised as potential refugia for the endangered owl species. Further research should include more focus on the potential refugia and propose which management measures should be undertaken to protect these owl species. Potential refugia would be beneficial to other alpine and forest specialist species that share similar habitat, but are not competitors for the same resources with the endangered owl species to avoid causing the contradictory effect.

3.4. Research IV

In this study we investigated spatial distribution and habitat overlap of five *Columbidae* family (Feral pigeon (*Columba livia forma domestica*), stock dove (*Columba oenas*), wood pigeon (*Columba palumbus*), Eurasian collared dove (*Streptopelia decaocto*), and European turtle dove (*Streptopelia turtur*)) present in Czechia, considering land use composition and land use heterogeneity. For the purpose of the study we used presence and absence data from the Bird Breeding Monitoring Program in 2015 and 2016 (Janda and Šťastný, 1984) for five *Columbidae* species. Furthermore, the land use map of the study area was provided by the Nature Conservation Agency of the Czech Republic as the consolidated layer of ecosystems (CLE). Besides land-use types, we calculated two more metrics: land-use richness and edge density. For more detailed methodology see Annex 4.

We confirmed that all five investigated *Columbidae* species highly overlapped in farmlands, followed by forests and urban areas. Besides, we registered almost complete overlap between *Columba livia* and *Streptopelia decaocto*, also *Columba palumbus* and *Streptopelia turtur*. Moreover, habitat utilisation matrix showed clear patterns that *Columba livia* and *Streptopelia decaocto* preferred urban areas and farmlands over any other land use type, whereas *Columba palumbus* and *Columba oenas* mostly inhabited all forest types and avoided farmlands and urban areas. Finally, *Streptopelia turtur* preferred farmlands and avoided urban areas.

Our GLM results showed that species *Columba livia* and *Streptopelia decaocto* were both positively associated with high edge density land use types, such as urban areas. Since both species are common in urban bird communities across Europe this result is not surprising (Evans et al., 2009). Regarding other species habitat overlaps, *Columba palumbus* and *Streptopelia turtur* overlapped mainly in farmlands. Although, *Columba palumbus* used to be a forest specialist across the continent, in the early 19th century it began colonising other available habitats such as farmlands and urban areas in Western and Central Europe, due to its adaptability to different habitats (Fey et al., 2015; Gibbs et al., 2010). Although results from our GLM did not show positive association of *Columba palumbus* with the urban areas, species was present in cities, and it is a well-known fact that it is common in urban bird communities. Thus, we can say that our results can be explained by the following two speculations: (i) the data is bias and there were not enough sampling points in cities, or (ii) the lengthy process of colonisation in Czechia is not finalised yet since there is evidence that it started later than in Western European countries (Evans et al., 2010). The process of urban colonisation is consists of three distinctive stages (i) arrival to urban areas, (ii) adjustment to the conditions, and (iii) spread within urban areas and to neighbouring similar habitats (Evans et al., 2010). When it comes to *Columba palumbus* studies have shown that firstly it colonised urban areas in Western, then Central (Witt et al., 2005), and then Eastern Europe (Bea et al., 2011). Still, when comparing *Columba palumbus* with other *Columbidae* species, such as *Streptopelia turtur* and *Columba oenas*, species is well adapted to urban areas where its abundance has been increasing (BirdLife International, 2021b; Richardson et al., 2022). This is most probably due to the differences in nesting requirements between species, since *Columba palumbus* requires open nests on branches which is available in urban areas. Whereas *Columba oenas* nests in tree cavities which are not common in cities and *Streptopelia turtur* nests in shrubs and trees and is not adapted to human disturbances (Gibbs et al., 2010). Regarding *Columba oenas*, high habitat overlap occurred with *Streptopelia turtur*, due to the similarity of their diet. Although, *Columba oenas* has been recognised as a forest specialist in Czechia (Koleček et al., 2010), it is a granivorous species that feeds on farmlands (Gibbs et al., 2010). However, when it comes to *Streptopelia turtur* it does not occupy closed-canopy forests but prefers open grounds and is associated with farmlands. Also, it has not adapted to cities such as other closely related *Columbidae* species (Gibbs et al., 2010).

Although our focus was on quantifying niche overlap of five species which are not endangered or of conservation concern, we tested the methodology on these species due to data availability. However, quantifying niche overlap is an important tool in bird species conservation since it can help identify competition for resources and species interactions and implement appropriate conservation strategies where necessary. Consequently, endangered species could benefit from this method as well, and vice versa by the "umbrella effect" endangered species could protect other species or habitats (Van Der Sluis et al., 2016). Secondly, knowledge of niche overlap provides information on species role in the ecosystem and helps to identify keystone species, the ones that play an essential role in ecosystem functioning. Furthermore, quantifying niche overlap and how they use their resources can predict species respond to climate change. Since the changes in availability of resources can lead to changes in distribution and abundance of different species. Finally, studying niche overlap provides information on ecosystem function, for instance if there is a high niche overlap between two species it is possible the ecosystem is less stable and prone to disturbances.

Overall, our study cannot significantly contribute to species conservation, however it provides methodology that can be useful in quantifying niche overlap. The results showed that *Columbidae* mainly overlap in urban areas, forests, and farmlands. With the highest species richness in urban areas. It is worth mentioning that not one sampling point had all the five species present, which shows that certain species avoided each other due to competition for similar resources. As for conservation implications of the study, it should be investigated if *Streptopelia turtur* could be used as an umbrella species for protecting other farmland birds.

3.5. Conclusions

When summarising the conclusions, from the above discussed four articles, it is important to keep in mind that the applied methods can have conservation implications if used correctly and with appropriate datasets. During the preparation of articles, to the best of my knowledge species data was of high quality and collected methodologically e.g., Bird Breeding Monitoring Programme and Spanish Atlas of Breeding Birds.

In general, our results support that protected areas are one of the cornerstone methods in species conservation. We suggest that protected areas mitigate negative effects of landscape changes, as well as that they support higher bird species richness. However, when looking at the specific components of bird diversity inside protected areas, effectiveness depended on the land use type and there was mismatch between bird diversity components. Although, all bird diversity metrics were high inside protected areas.

Furthermore, performed SDMs on two endangered owl species allowed us to investigate the current and future potential species habitats, as well as species potential refugia in the face of climate change. Our study shows that species area will be shrinking in the future and improvement of species conservation in the Balkan Peninsula is necessary. Furthermore, refugia might contribute in case that conservation measures are taken into action and managed according to species needs. Our results are valuable in the Balkan Peninsula for future species conservation decisions and efforts, however conservation actions, such as improvements of habitat protection, are urgent.

Finally, the simple methodology performed in the niche overlap research can be applied on species of conservation importance too as it provides preliminary look at the utilisation of specific land use types by each species, and species association with it. From a different conservation perspective, *Streptopelia turtur* could serve as an umbrella species to other farmland species, specifically in lowering the hunting pressure on these endangered species. Besides, our study presented these common species habitat affinities and utilisation. However, more detailed analysis is necessary to understand the co-existence of these species in overlapping habitats and the potential interspecific competition between certain species that did not overlap.

Each methodology had its own advantages and disadvantages, however if for instance we combined methods from two studies focusing on protected areas, results could provide more detailed insight into the performance of protected areas and underlying processes of lower species richness inside protected areas in 2014/2015. As well as, protected areas focusing on specific species could be analysed with SDMs and their potential expansion predicted. Furthermore, our results provided valuable information for future conservation plans in countries where studies were conducted.

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5. Curriculum vitae & list of publications

Personal

Name: Kristina Cerman
Date of birth: January 12*th*, 1993 (*Serbia*)
E-mail: floigl@fzp.czu.cz
ORCID: https://orcid.org/0000-0002-9442-1230
RG: https://www.researchgate.net/profile/Kristina-Cerman

Affiliation

2018 – present
Department of Ecology,
Faculty of Environmental Sciences,
Czech University of Life Sciences Prague
Member of Community Ecology & Conservation

Education

2018 – present
Department of Ecology,
Faculty of Environmental Sciences,
Czech University of Life Sciences Prague
PhD studies in Applied and Landscape Ecology
Thesis topic: *Applying different methods for bird conservation across European countries*

2016 – 2018
Department of Applied Geoinformatics and Spatial Planning,
Faculty of Environmental Sciences,
Czech University of Life Sciences Prague
Master's degree in Nature Conservation
Thesis topic: *Spatial pattern of bird diversity and community metrics in two protected areas of Northern Spain*

2011 – 2016
Department of Ecology and Biology,
Faculty of Sciences,
University of Novi Sad
Bachelor's degree in Ecology

Participation in Research Projects

2020
Project title: *Are protected areas safeguarding avian communities in the Czech Republic?*
Internal Grant Agency of the Faculty of Environmental Sciences
Czech University of Life Sciences Prague
Position: project Leader

Internships

06/2022 – 08/2022
Pablo de Olavide University
Sevilla, Spain

Publications in Journals with Impact Factor (J_{imp})

1. Floigl, K., Benedetti, Y., Reif, J., Voříšek, P., Morelli, F., 2022. Assessing protected area network effectiveness through the temporal change in avian communities' composition. Journal for Nature Conservation 68. https://doi.org/10.1016/j.jnc.2022.126222
2. Morelli, F., Benedetti, Y., Floigl, K., Ibáñez-Álamo, J.D., 2021. How are Natura 2000 protected areas covering different components of avian diversity in Spain? Ecological Indicators 133, 108452. https://doi.org/10.1016/j.ecolind.2021.108452
3. Cerman, K., Rajković, D., Topić, B., Topić, G., Shurulinkov, P., Mihelič, T., Delgado, J.D., 2022. Environmental Niche Modelling Predicts a Contraction in the Potential Distribution of Two Boreal Owl Species under Different Climate Scenarios. Animals 12, 1–17. https://doi.org/10.3390/ani12223226
4. Floigl, K., Benedetti, Y., Reif, J., Morelli, F., 2022. Spatial Distribution and Habitat Overlap of Five Columbidae Species in the Czech Republic. Animals 12. https://doi.org/10.3390/ani12060743

Teaching Experience

2018 – 2022
Department of Applied Geoinformatics and Spatial Planning
Seminars of GIS I

International Conferences

04/2019
Poster title: *Exploring temporal changes of avian community composition: differences between farmland and forest habitats*
Floigl K., Benedetti Y., Reif J., Morelli F.
Conference: Counting Bird Counts, Bird Numbers 2019.
Evora, Portugal.

6. Annex section

Annex 1. Assessing protected area network effectiveness through the temporal change in avian communities' composition.

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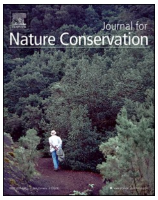

Assessing protected area network effectiveness through the temporal change in avian communities' composition

Kristina Floigl[a], Yanina Benedetti[a], Jiři Reif[b,c], Petr Voříšek[c,d], Federico Morelli[a,e,*]

[a] Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Community Ecology & Conservation, Kamýcká 129, Praha – Suchdol 165 00, Czech Republic
[b] Institute for Environmental Studies, Faculty of Science, Charles University, Prague, Benatska 2, 128 01 Prague 2, Czech Republic
[c] Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacky University in Olomouc, 17. Listopadu 50, 771 46 Olomouc, Czech Republic
[d] Czech Society for Ornithology, Na Bělidle 34, 150 00 Praha 5, Czech Republic
[e] Institute of Biological Sciences, University of Zielona Góra, Prof. Z. Szafrana St. 1, 65-516 Zielona Góra, Poland

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Protected areas

ABSTRACT

Current rates of land use are driving temporal changes in avian communities. Thus, it is essential to properly designate and manage protected areas since they mitigate the adverse effects of temporal changes on species populations. By using common bird monitoring data in Czechia from two periods (2005/2006 and 2014/2015), we calculated two indices of temporal change per each site, the Jaccard dissimilarity index (temporal dissimilarity between the community composition) and the difference in bird species richness between both periods (delta bird species richness). We tested three main predictions on temporal change in bird communities between protected and unprotected areas: (i) bird species richness will be higher inside protected areas, (ii) temporal changes in avian communities will be lower inside protected areas, (iii) the effect of protected areas will interact with land-use types, land-use richness, and altitudinal zones. Bird species richness was higher inside protected areas in 2014/2015, ten years after the implementation of Natura 2000 in Czechia. Both indices of temporal change were lower inside protected areas. The interactions of protected areas and land-use types on the indices of temporal change were not significant. However, interactions with altitudinal zones had a significant positive effect on the indices, i.e., in higher altitudes, delta bird species richness and higher dissimilarity levels. Our study underlines the importance of protected areas for conservation by buffering the consequences of factors driving temporal community changes. Together, our results indicate a positive 'umbrella' effect of protected areas on avian communities that was likely facilitated by the implementation of Natura 2000.

1. Introduction

An essential key for species conservation is adequately designed and effectively managed protected areas (Coad et al., 2015) since species benefit from the protection provided by the legislation (Koschová, Rivas-Salvador, & Reif, 2018). One of the reasons the EU designated the Natura 2000 network was to implement the Birds and Habitat Directives adopted in 1979 and 1992, respectively. Sites of Community Interest (SCIs) are protecting species listed in the Habitat Directive (Habitat Directive - Council Directive 92 /43 /EEC of 21 May 1992 on the Conservation of Natural Habitats and Wild Fauna and Flora, 2019). Besides, Special Protection Areas (SPAs) are designed to protect endangered bird species listed in Annex I of the Birds Directive and migratory species (Birds Directive - Council Directive 79/409/EEC of 30 November 2009 on the Conservation of Wild Birds, 2009). Both directives are complementary and constitute the Natura 2000 network, which currently covers 18% of the EU's territory (European Environment Agency, 2019).

Even though the European Biodiversity report recognised that biodiversity is an essential value for both economy and citizens' well-being (European Environment Agency, 2019), studies that utilise long-term monitoring records to assess protected areas' effectiveness in conserving biodiversity are still limited (Gaston et al., 2006). Consequently, the ability of protected areas in supporting species populations is still a significant knowledge gap in protected-area research (Gaston, Jackson, Cantú-Salazar, & Cruz-Piñón, 2008). The results of some studies suggested that protected areas can deliver overall positive

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* Corresponding author at: Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Community Ecology & Conservation, Kamýcká 129, Praha – Suchdol 165 00, Czech Republic.
E-mail address: fmorellius@gmail.com (F. Morelli).

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outcomes for the conservation of habitat and populations (Devictor, Godet, Julliard, Couvet, & Jiguet, 2007; Pellissier et al., 2019) and increase populations of endangered species (Paul F. Donald et al., 2007). Also, several studies indicated that protected areas mitigate adverse effects of human-induced threats (Watson, Dudley, Segan, & Hockings, 2014). For instance, under the current climate change, protected areas may represent refugia for bird communities (Gaüzère, Jiguet, & Devictor, 2016) by mitigating species' local extinctions and abundance losses (Lehikoinen, Santangeli, Jaatinen, Rajasärkkä, & Lehikoinen, 2019). Additionally, landscapes inside protected areas should be subjected to fewer sources of disruption and therefore foster more stable habitats, although land-use changes inside protected areas need monitoring to prevent from affecting species conservation (Hermoso, Morán-Ordóñez, & Brotons, 2018). On the other hand, protected area networks should focus on conserving natural processes, such as evolutionary and ecological processes of species which are essential aspects in biodiversity conservation (Maiorano, Falcucci, Garton, & Boitani, 2007).

The current rates of land-use changes (Donald, Green, & Heath, 2001; Newbold et al., 2015), habitat fragmentation (Haddad et al., 2015), and climate change (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012) are driving temporal changes in global biodiversity. A large body of literature has reported a decline in European bird populations due to these drivers (Frenzel, Everaars, & Schweiger, 2016). Thus, studying temporal changes is essential for providing more in-depth insight into species populations, which is beneficial for future conservation plans and adequate species protection (Koleček, Reif, Štastný, & Bejček, 2010; Latta, Tinoco, Graham, & Graham, 2011). To better understand the underlying mechanisms of the temporal changes, it is useful to consider land-use types and richness (Duelli, 1997) and altitudinal zones (Chamberlain, Brambilla, Caprio, Pedrini, & Rolando, 2016) in the analyses. Concerning the land-use types, it is important to realise that each land-use type changes over time, influencing bird communities (Morante-Filho, Arroyo-Rodríguez, Pessoa, Cazetta, & Faria, 2018). Changes such as agricultural intensification (Donald, Sanderson, Burfield, & van Bommel, 2006) are decreasing numbers of specialist bird species, which showed to be more susceptible to land-use changes than generalists (Devictor, Julliard, & Jiguet, 2008; Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006). Therefore, it is important to maintain higher land-use richness, defined by the number of different habitat patches per unit area (Duelli, 1997). It increases the species richness (MacArthur & MacArthur, 1961) and minimises the adverse effects of land-use changes on bird communities by increasing niche availability (Tscharntke et al., 2012). Regarding the altitudinal zones, primary drivers of the differences in species communities across altitudinal gradients are temperature, vegetation, space and food availability (Sam, Koane, Bardos, Jeppy, & Novotny, 2019). For instance, mountains foster unique habitats with small-range specialist species making them more sensitive to habitat loss and more prone to the risk of extinction (Rivas-Salvador, Hořák, & Reif, 2019). Furthermore, higher altitudes provide less disturbed landscapes by human activities, such as agriculture, mostly confined to lowlands. Therefore, regarding protected areas, conservation actions should have a more significant effect on lowlands due to a higher ecological contrast between inside and outside protected areas (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011).

The main goal of this study was to analyse temporal changes of bird communities in a ten-year interval concerning environmental variables: (1) inside or outside the protected areas, (2) land-use types and landscape heterogeneity and (3) altitudinal zones, in Czechia. For this purpose, we used data from the national Breeding Bird Monitoring Program in Czechia (Janda & Šťastný, 1984a) and calculated temporal change in bird species richness (delta bird species richness) and Jaccard dissimilarity index (Chao, Chazdon, & Shen, 2005). We tested both indices of temporal change, and whether they were significantly affected by the environmental variables. If the bird population benefits from protected areas, we expect a lower temporal change in avian communities' composition and higher bird species richness inside protected areas than outside. Also, the influence of protected areas should interact with environmental variables. Due to the smaller ecological contrast between inside and outside of protected areas in higher altitudes, more heterogeneous and less disturbed landscapes, we expect a smaller effect of protected areas on temporal changes of bird communities in these landscapes (Kleijn et al., 2011).

2. Methods

2.1. Study area and protected areas network

The study was carried out in Czechia, which covers an area of 78,865 km^2. The land composition of the country is primarily forests (33,835 km^2) and farmlands (12,806 km^2). In the temperate climate zone, the country characterised by a moderately continental climate, with mild, humid summers with occasional hot spells, cold, cloudy, and humid winters (Sadlo & Storch, 2000).

The protected areas in Czechia consist of Natura 2000 Network and national protected areas, both designated according to Act No. 114/1992 Coll. (Anonym, 2004). Consequently, the country's list of protected areas contains both Natura 2000 and national sites, even though around 7,000 km^2 of these areas overlap in Czechia (Agentura ochrany přírody a krajiny České Republiky, 2020). National protected areas consist of national parks, protected landscape areas, nature reserves, national nature reserves and nature monuments as protected categories (Anonym, 2004). National parks and protected landscape areas are extensive territories of natural ecosystems with restricted human activities and human recreational activities that do not damage the natural values, respectively. Whereas nature reserves, national nature reserves and nature monuments are smaller territories of natural ecosystems and habitats for endangered species (Anonym, 2004). Currently, 13,435 km^2 (17%) of Czechia is under national protection, and 11,148 km^2 (14%) of the land is under the Natura 2000 network (SPAs and SCIs)(European Environment Agency, 2019).

2.2. Bird data collection and land use composition around the sampling points

Avian data were collected in sampling sites scattered throughout Czechia (Fig. 1) within the Breeding Bird Monitoring Program (Janda & Šťastný, 1984b). The Breeding Bird Monitoring Program is conducted by skilled voluntary ornithologists using the point counts (Bibby, Burgess, Hill, & Mustoe, 2000) at each site. Each site consists of 20 sampling points located 300–500 m apart. Birds are counted twice per breeding season at each sampling point to cover both early and late breeders. During each visit, all birds detected visually and acoustically are counted for 5 min at each sampling point. For purposes of this study, we considered only the counts within a 100-meter radius around each sampling point. Although the selection of sample plots is free, i.e., fieldworkers decided where to set up a plot, our study covers the whole country, considering different land use and altitudinal zones of sampling points.

The land-use map of the study area was provided by the Nature Conservation Agency of the Czech Republic as the Consolidated Layer of Ecosystems (CLE). CLE is based on a country-wide habitat mapping performed during the early 2000 s and updated up to 2018 (Hönigová & Chobot, 2014).

We used ArcGIS 10.5.1 (ESRI, 2011) to do spatial data analysis on CLE in five stages:

1. Calculation of 100-meter buffer around each sampling point and intersecting the buffer areas with the land cover map.

2. Calculation of land-use richness for each 100-meter buffer as the number of different land-use types (Duelli, 1997).

3. Estimating land-use composition by calculating all land use types in each buffer. Land-use was grouped into six categories: forest, grassland (natural), farmland (mainly arable land), wetland riparian and

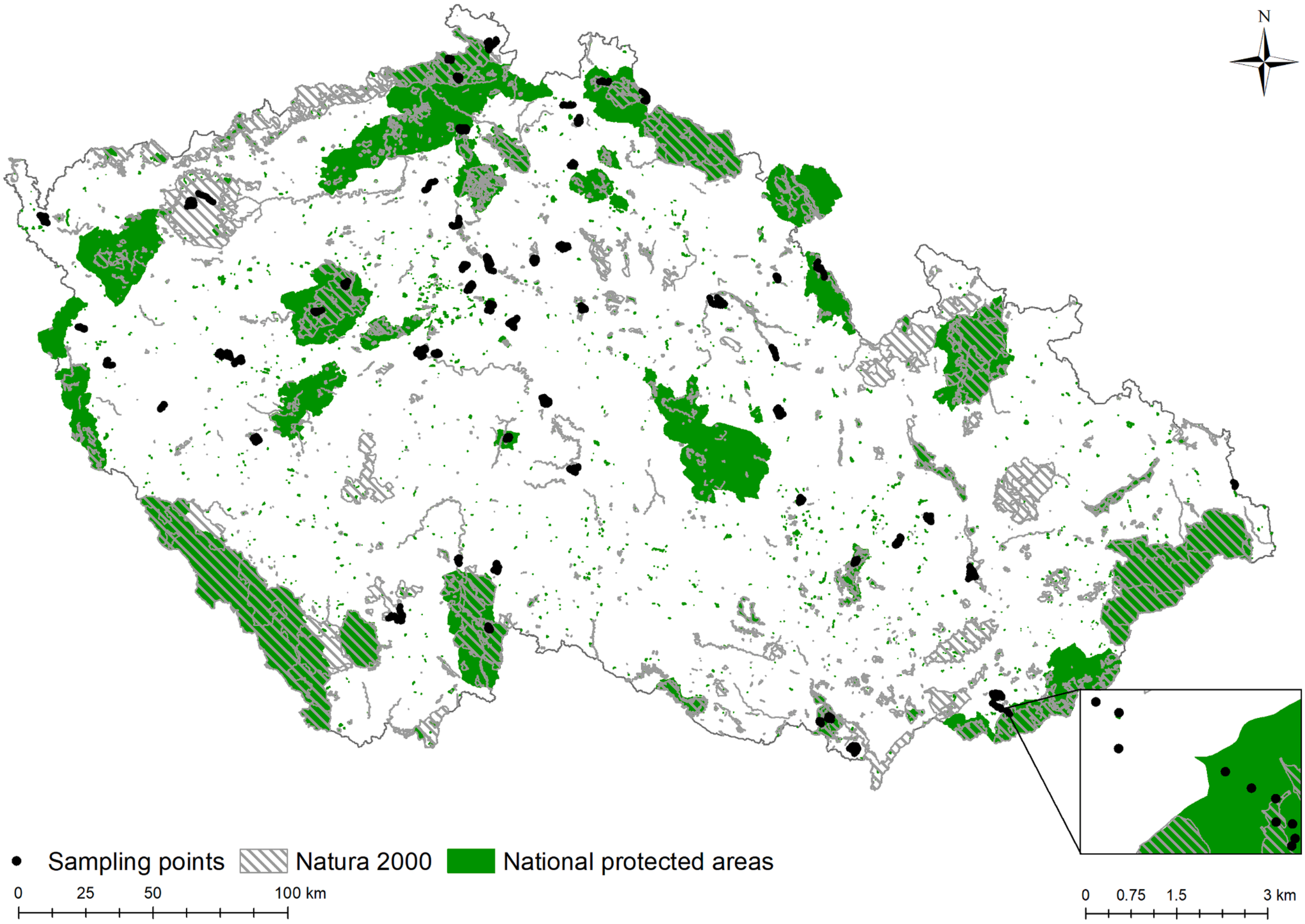

Fig. 1. Study area (study sites represented as black dots, n = 1209; each site contains 20 sampling points that are not shown) and protected areas in Czechia.

urban (see Table S2).

4. Classification of buffers in terms of dominant environment, each buffer was classified in the following categories: bare land (mostly in urban areas), farmland, forest, natural grassland, and wetland riparian when the land cover of each category was>60%. Otherwise, it was classified as a mixed environment (Morelli et al., 2013). Land use composition of sampling points in Czechia mainly consisted of forest (37%), farmland (27%) and mixed environments (20%).

5. Finally, sampling points were classified into three categories according to their altitude: lowland (150–300 m); hill (300–650 m); mountain (>650 m) following Hanzelka et al. (2015).

2.3. Assessment of temporal change in avian community composition

From the Breeding Bird Monitoring Program, we considered points counted both times, in 2005/2006 and 2014/2015 for this study, obtaining a total of 1,209 individual points. Sampling points were well-represented inside (441 points) and outside (768 points) of the borders of Czech protected areas (Fig. 1). For the categorisation of sampling points in protected areas see Table S1.

For analysing the temporal change in avian communities, we calculated two indices.

Firstly, we calculated the Jaccard dissimilarity index for assessing the compositional dissimilarity of avian assemblages between both periods (hereafter called "dissimilarity"), based on bird presence/absence data in each paired community. The values of absolute dissimilarity range from 0 to 1, and index values closer to 1 mean that communities are more different. Here we used the dissimilarity for analysing the temporal change of avian communities. The calculation of the index was performed with the function *vegdist* in package 'vegan' in R (Oksanen et al., 2018; R Development Core Team, 2019). The formula for calculating the Jaccard index is:

$$J = a/a + b + c$$

where a is the number of species common for both periods, b and c are the numbers of species unique for 2005/2006 and 2014/2015, respectively (Chao et al., 2005).

Secondly, we estimated bird species richness in each sampling point for 2005/2006 and 2014/2015 and then, we calculated the difference between both periods (delta bird species richness). The values of delta bird species richness can be positive (indicating the increasing number of species) or negative (indicating the decreasing number of species).

2.4. Statistical analyses

We compared bird species richness between 2005/2006 and 2014/2015; and community dissimilarity inside and outside of protected areas using a non-parametric Mann-Whitney test (Hodges & Lehmann, 1956). To explore the differences in delta bird species richness from inside and outside protected areas, we performed the Unpaired Two-Samples T-test (Altman, 1991).

Additionally, we performed a non-metric multidimensional scaling (NMDS) analysis using a Gower dissimilarity matrix to assess the dissimilarity of bird communities between inside and outside protected areas for 2005/2006 and 2014/2015. The NMDS technique is an indirect gradient analysis which produces an ordination based on a dissimilarity matrix, collapsing multi-dimensions of information into two dimensions (Mead, 1992). The stress in the NMDS representation is the disagreement between the two dimensions and the predicted values from the regression. Lower 2-D stress values indicate a better representation of the data (Oksanen et al., 2016). NMDS is considered a flexible ordination technique because of its lack of assumptions of linearity or normal distribution among variables (Zuur, Ieno, & Elphick, 2010). In the specific, the comparison using NMDS was performed comparing avian community matrices (species occurrence) inside and outside of the Czech protected areas during the first assessment (2005/2006) and then repeated for the second assessment (2014/2015).

To evaluate the changes in avian communities between 2005/2006 and 2014/2015 concerning the type of dominant environment, presence of protected areas, altitudinal zones and land-use richness, we used generalised linear models (GLM) (Burnham & Anderson, 2002). We modelled the two indices of community change (i.e., dissimilarity and delta bird species richness) separately.

The two response variables (dissimilarity and delta bird species richness) were fitted following a normal distribution after having explored their distribution using the Box-Cox transformation tool (Box & Cox, 1964), with the package 'MASS' (Venables & Ripley, 2002). A test of variance inflation factor (VIF) of the full candidate model was applied to check for potential multicollinearity issues among predictor variables, using the package 'fmsb' for R (Nakazawa, 2017). Only variables with VIF < 2 were introduced in the model procedures. Additionally, we tested potential spatial autocorrelation (SAC) issues in the dataset by applying a Mantel test (Mantel, 1967). The Mantel statistic (r_M) varies between -1 and $+1$. It behaves like a correlation coefficient (Fortin & Payette, 2002), evaluating the similarity between two matrices. The first matrix is calculated as a geometric distance, and the second one with the geographical distance among sampling sites (Legendre & Legendre, 2012). We tested for significance on the Mantel Test by running the Monte Carlo permutations with 999 randomisations (Oksanen et al., 2016).

We ran the models using the 'nlme' package for R (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017). In the first model, the response variable was avian community "dissimilarity". The predictors were the dominant environment, altitudinal zone (lowlands, hills, or mountains), protected area (inside or outside), and land use richness. Observations were not treated as statistically independent for modelling purposes because spatial autocorrelation was weak but significant (Mantel test, 999 randomisations: $r_M = 0.068$, simulated $p < 0.05$). In this case, a term to account for the spatial autocorrelation was added, and we ran the model as a generalised least squares (GLS) model (Im & Snow, 1993). Using the same set of predictors in the second model, we modelled delta bird species richness as the response variable. The respective models were formulated as follows:

(1) avian community "dissimilarity" ~ dominant environment * altitudinal zone * protected area + land-use richness.

(2) delta bird species richness ~ dominant environment * altitudinal zone * protected area + land-use richness.

No SAC problems were detected in the data (Mantel test, 999 randomisations: $r_M = 0.10$, simulated $p > 0.05$), then a GLM was used. In both cases, Akaike's Information Criterion (AIC) was used to determine the models that 'best' explained variation in the data (Burnham & Anderson, 2002).

All statistical tests were performed with R software version 3.5.1 (R Development Core Team, 2019).

3. Results

Overall, 192 species were recorded during the study period, out of which 56 species are listed in Annex I of the Birds Directive (see Table S3). In general, bird species richness was lower inside (n = 138) than outside (n = 152) of the protected areas. In the specific, bird species richness was significantly lower in 2005/2006 inside protected areas (mean = 15.7) than outside (mean = 16.1) of them. However, in 2014/2015, bird species richness was higher inside protected areas (mean = 17.7) than outside (mean = 16.1).

Overall, the temporal change of avian communities was lower inside in comparison to outside protected areas.

First, we detected a higher level of dissimilarity outside protected areas (Table 2, Fig. 2). In fact, dissimilarity had lower values inside than outside the protected areas (alternative = less, p-value = 0.003, Fig. S1), i.e., temporal change of avian communities was lower inside protected areas. Concerning land-use types, dissimilarity decreased in forests, urban, wetland riparian and mixed environments, as well as in more heterogeneous landscapes, characterised by high land-use richness (Table 2, Fig. 2). Dissimilarity was higher in hills and mountains than in lowland zones (Table 2, Fig. 3). Finally, absolute dissimilarity significantly decreased outside the protected areas in hills and mountains (Table 2, Fig. 3).

Second, we found a decrease in the delta bird species richness outside protected areas (Table 3, Fig. 4) and higher values inside the protected areas (alternative = greater, p-value = 7.8e-14,), i.e., the increase in species richness was greater in protected areas. Additionally, delta bird species richness showed overall negative mean values outside the protected areas (see Fig. S2). Concerning land-use types, there was a negative association between the delta bird species richness and mixed environments (Table 3, Fig. 4). When investigating interactions with different altitudinal zones, the delta bird species richness significantly increased in hilly zones outside the protected areas (Table 3, Fig. 5).

The results of the NMDS ordination based on bird community composition shows a relatively lower variability between avian communities of inside and outside protected areas in the period 2014/2015 than in the period 2005/2006 (Fig. S3). This result indirectly indicates a relatively higher temporal homogenization of species assemblages. During the second assessment (2014/2015) bird communities tend to be more similar inside and outside the network of protected areas, as indicated by slightly lower stress (Fig. S3).

4. Discussion

Our results support our predictions that bird species richness will be higher, and the temporal changes in bird communities will be lower inside than outside protected areas. However, a significant interaction with altitude indicated that the lower temporal changes inside (rather than outside) protected areas were confined to lowlands. Similarly, the positive effect of protected areas on delta bird species richness seems to be less clear in the mountains. Furthermore, delta bird species richness showed a significant negative association with mixed environments.

Table 1
The number of study sites inside (n = 441) and outside (n = 768) protected areas per each altitude zone and dominant environment.

Inside protected areas				
Dominant environment	Lowland	Hill	Mountain	Total
Farmland	23	31	0	54
Forest	49	95	34	178
Grassland	8	1	1	10
Mixed	45	84	6	135
Urban	0	2	0	2
Wetland riparian	31	22	9	62
Total	156	235	50	**441**

Outside protected areas				
Dominant environment	Lowland	Hill	Mountain	Total
Farmland	101	108	1	210
Forest	33	101	2	136
Grassland	0	3	0	3
Mixed	136	186	4	326
Urban	41	35	0	76
Wetland riparian	8	9	0	17
Total	319	442	7	**768**

Table 2
Results of the GLS model, accounting for temporal changes in the avian community between 2005/2006 and 2014/2015, measured as "dissimilarity" concerning the interactions between the dominant environment, altitudinal zone (lowlands, hills, or mountains) and protected area (inside or outside), plus land use richness. Abbreviations: SE – standard error. Significant variables are highlighted in bold.

Variables	Estimate	SE	t values	P-values
(Intercept)	0.541	0.012	43.659	<0.001
PA (outside)	**0.095**	**0.012**	**7.623**	**<0.001**
Zone (hills)	**0.117**	**0.013**	**9.241**	**<0.001**
Zone (mountains)	**0.096**	**0.020**	**4.869**	**<0.001**
Dominant environment (forest)	**−0.094**	**0.009**	**−10.191**	**<0.001**
Dominant environment (grassland)	−0.039	0.035	−1.124	0.2611
Dominant environment (mixed)	**−0.036**	**0.011**	**−3.323**	**0.001**
Dominant environment (urban)	**−0.089**	**0.017**	**−5.330**	**<0.001**
Dominant environment (wetland/riparian)	**−0.040**	**0.014**	**−2.880**	**0.004**
Land use richness	**−0.001**	**0.000**	**−2.197**	**0.028**
PA (outside): Zone (hills)	**−0.131**	**0.015**	**−8.491**	**<0.001**
PA (outside): Zone (mountains)	**−0.165**	**0.050**	**−3.305**	**0.001**

Finally, land-use richness significantly affected negatively the temporal dissimilarity of avian communities, but not delta bird species richness.

Overall, from 2005/2006 to 2014/2015, bird species richness increased, and temporal changes were less pronounced inside protected areas (Table 2, Table 3) in Czechia. This pattern suggests that the species benefited from the network of protected areas, incl. N2000 sites. Since SPAs aim to protect endangered species, listed in Annex I of the EU's Birds Directive and guarantee their specific nesting, breeding, and feeding needs (Paul F. Donald et al., 2007), the increase in bird species richness upon the network implementation was anticipated and in line with records from other EU states (Donald et al., 2007; Sanderson et al., 2016). Indeed, a positive effect of listing under Annex I was recently reported from the so-called new EU-member states, including Czechia (Koschová et al., 2018). However, our study is limited by examining two periods with a ten-year difference, therefore we cannot state that we analysed a ten-year trend.

Moreover, the conservation benefits of the Natura 2000 network may concern the other species too and human-impacted habitats, such as arable lands (Brodier, Augiron, Cornulier, & Bretagnolle, 2013). However, a study by Santana et al. (Santana et al., 2014) detected a gap in the Natura 2000 network's ability to protect less charismatic species of ecological importance. We cannot test this in arable lands in Czechia due to the absence of large-scale protected areas in this type of land-use. On the other hand, a recent study by Pellissier et al. (Pellissier et al., 2019) reported an increase in the abundance of bird species not listed in Annex I inside the Natura 2000 network due to the beneficial 'umbrella' effects of the legal protection of endangered species (Van Der Sluis et al., 2016). Additionally, protected areas foster more suitable habitats for species by protecting landscapes (Brodier et al., 2013; Watson et al., 2014) and

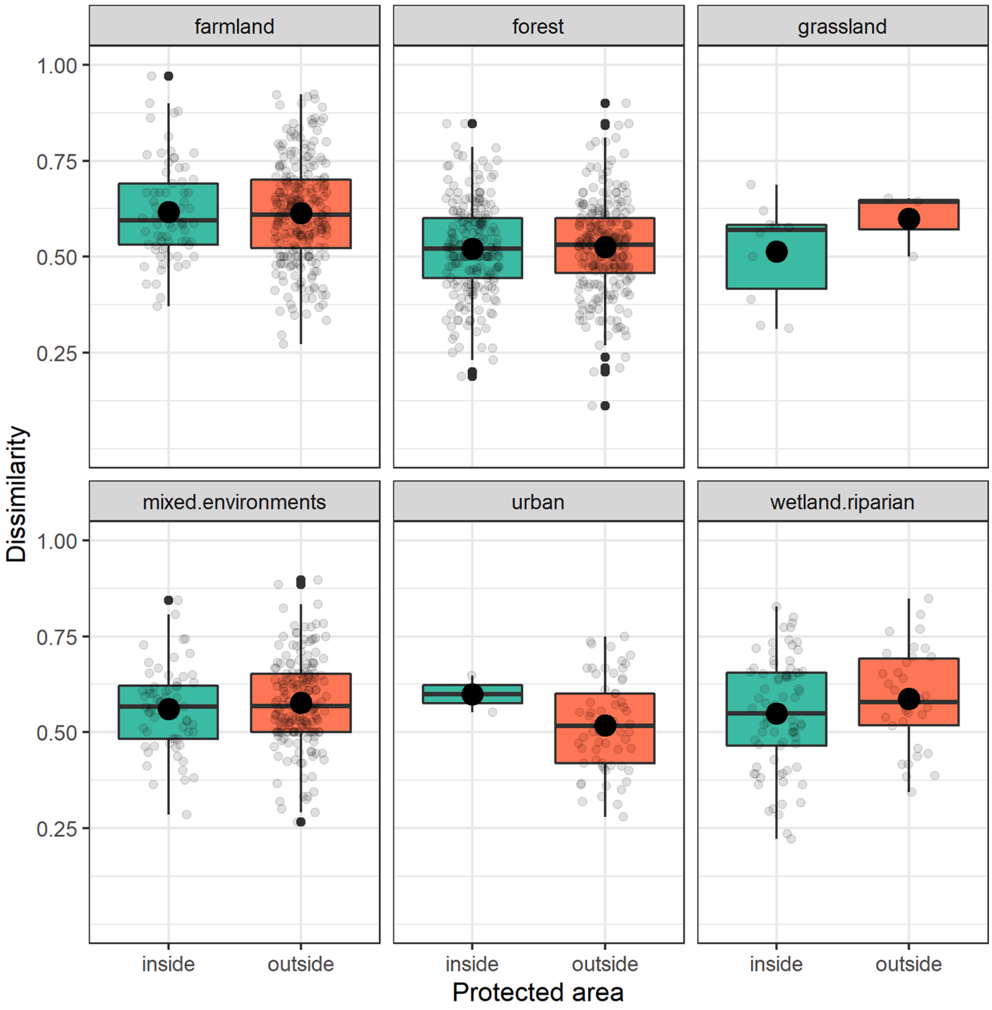

Fig. 2. Temporal changes in avian community between 2005/2006 and 2014/2015, measured as "dissimilarity" in relation to different types of dominant environment inside (farmland, n = 54; forest, n = 178; grassland, n = 10; mixed, n = 135; urban, n = 2; wetland riparian, n = 62) and outside (farmland, n = 210; forest, n = 136; grassland, n = 3; mixed, n = 326; urban, n = 76; wetland riparian, n = 17) protected areas in Czechia.

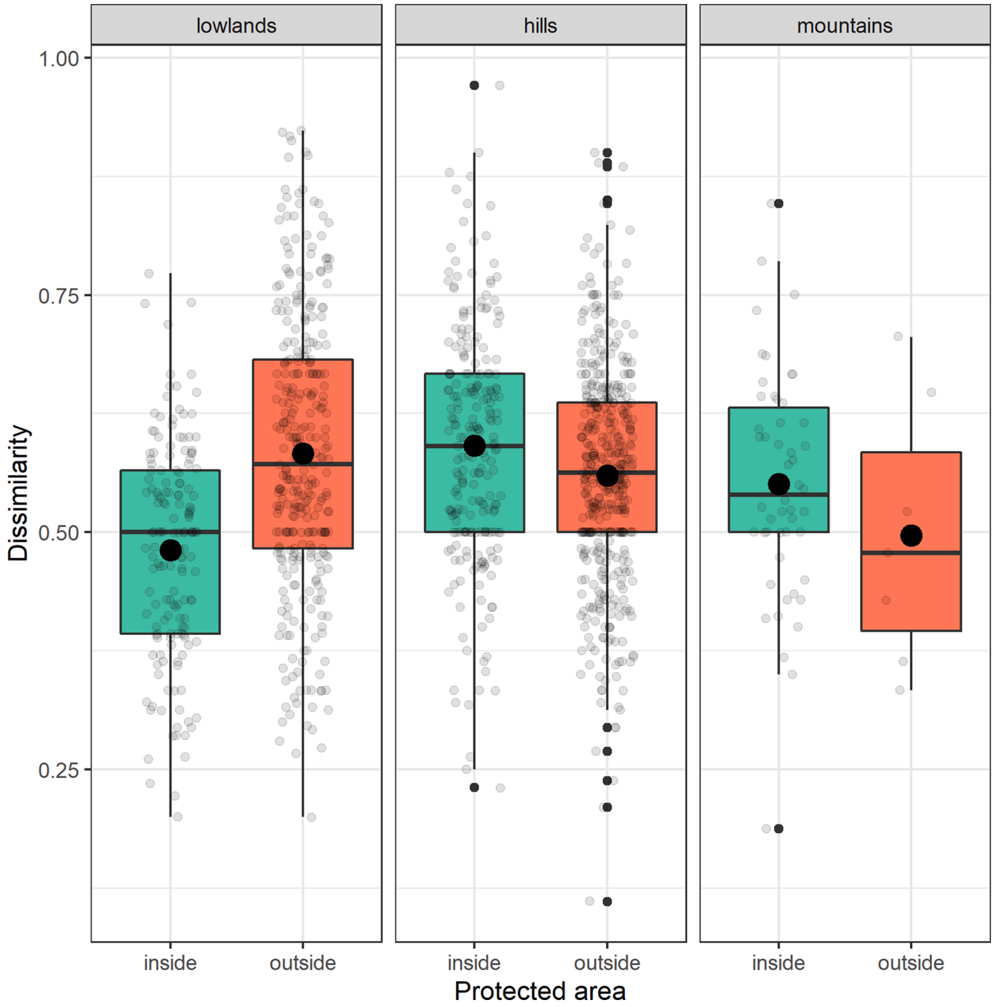

Fig. 3. Temporal changes in avian community between 2005/2006 and 2014/2015, measured as “dissimilarity” in relation to altitudinal zones inside (lowlands, n = 156; hills, n = 235; mountains, n = 50) and outside (lowlands, n = 319; hills, n = 442; mountains, n = 7) protected areas in Czechia.

Table 3
Results of GLM, accounting for temporal changes in the avian community between 2005/2006 and 2014/2015, measured as “delta bird species richness” concerning the interactions between dominant environment, altitudinal zone (lowlands, hills, or mountains) and protected area (inside or outside), plus land use richness. Abbreviations: SE – standard error. Significant variables are highlighted in bold.

Variables	Estimate	SE	t values	P-values
(Intercept)	2.633	0.673	3.911	9.2e-05
Dominant environment (forest)	−0.627	0.495	1.265	0.206
Dominant environment (grassland)	0.103	1.857	0.056	0.956
Dominant environment (mixed)	**−1.760**	**0.588**	**2.99**	**0.003**
Dominant environment (urban)	0.913	0.910	1.002	0.316
Dominant environment (wetland/ riparian)	−1.432	0.737	1.94	0.052
Land use richness	0.042	0.022	1.888	0.059
PA (outside)	**−4.523**	**0.667**	**6.776**	**<0.001**
Zone (hills)	0.170	0.676	0.252	0.801
Zone (mountains)	−0.450	1.060	0.424	0.671
PA (outside): Zone (hills)	**2.355**	**0.826**	**2.847**	**0.004**
PA (outside): Zone (mountains)	4.578	2.682	1.705	0.088

mitigating the adverse effects of climate change (Gaüzère et al., 2016). Therefore, protected areas provide more stable ecosystems, with fewer environmental changes, by applying necessary management strategies, which support higher species richness (Watson et al., 2014). On the other hand, the lower bird species richness outside protected areas in 2014/2015 is congruent with previous studies showing that the Act on Nature Conservation and Landscape Protection in the Czech Republic and EU’s Directives failed to improve the overall status of species with the lowest protection status or the species without it (Voříšek, Reif, Šťastný, & Bejček, 2008).

When focusing on the effects of different altitudinal zones inside and outside protected areas on avian communities, both indices of temporal change indicated significantly more similar communities outside the protected areas in hills (Fig. 3, Fig. 5). Furthermore, levels of dissimilarity were significantly lower outside the protected areas in the mountains, i.e., communities were more similar outside protected areas in the mountains. We suggest one of the drivers of this pattern is the overrepresentation of protected areas in highlands and avoidance of agricultural lowlands (Maiorano et al., 2007) since the effect of protected areas is considered to be less evident at higher altitudes compared to heavily exploited unprotected areas in lowlands where the ecological contrast between inside and outside of protected areas is higher (Kleijn et al. 2011). Alternatively, sites outside of the protected areas may be less disturbed at higher altitudes due to generally lower human population density and economic activities (Václavík & Rogan, 2009). We suggest that all these possibilities may act together.

Avian communities from 2005/2006 and 2014/2015 were more similar in forests, wetland riparian, urban and mixed environments, as well as in heterogeneous landscapes (Table 1). Low temporal changes found in forests may be because forests have longer management cycles

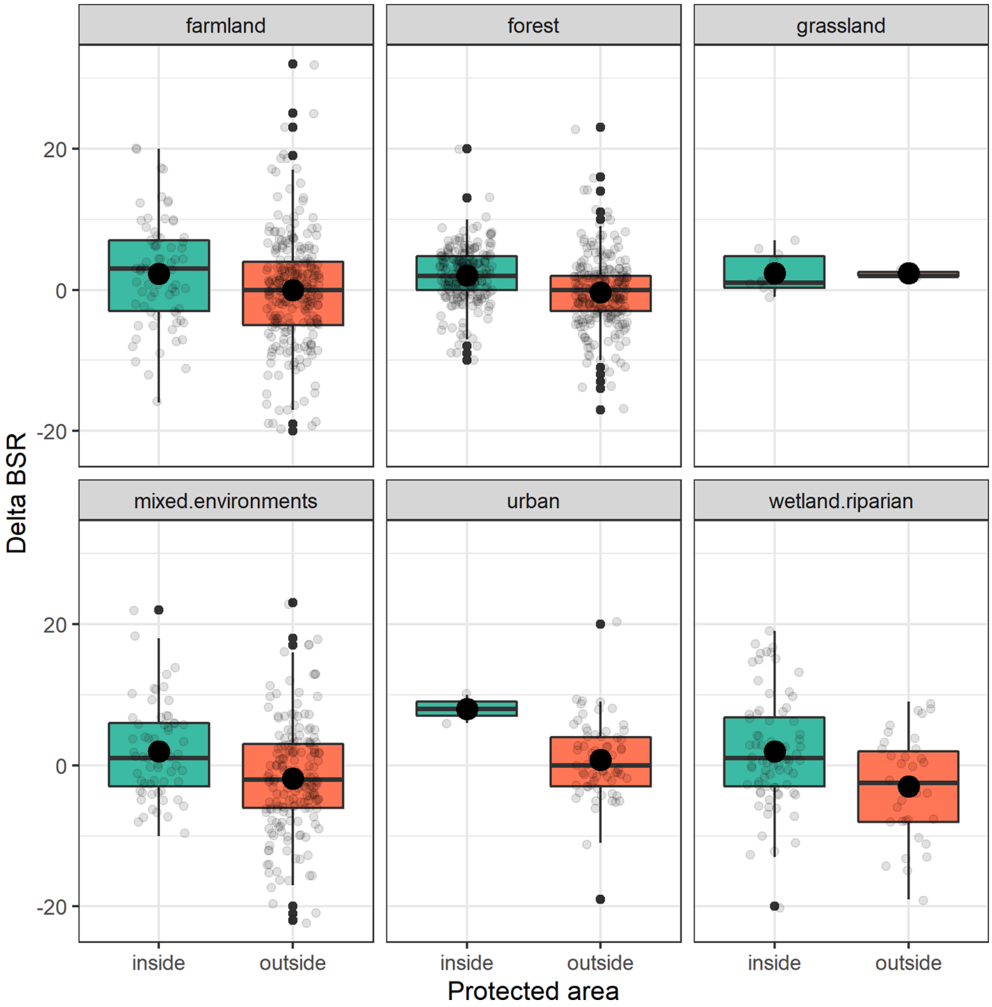

Fig. 4. Temporal changes in avian community between 2005/2006 and 2014/2015, measured as "delta bird species richness" (delta BSR) in relation different types of dominant environment inside (farmland, n = 54; forest, n = 178; grassland, n = 10; mixed, n = 135; urban, n = 2; wetland riparian, n = 62) and outside (farmland, n = 210; forest, n = 136; grassland, n = 3; mixed, n = 326; urban, n = 76; wetland riparian, n = 17) protected areas in Czechia.

than farmlands and forests are ecologically a more natural and stable type of habitat, which provides less environmental changes than other habitats associated more with human activities, such as farmlands (Morelli, Benedetti, Perna, & Santolini, 2018). An extensive analysis on the European scale shows the relative stability of common forest birds from 1980 to 2015 (Gregory, Škorpilová, Voříšek, & Butler, 2019). However, in the past ten years, bark beetle outbreaks (*Ips typographus*, Linnaeus 1758) in Czechia (Fiala et al., 2019) have led to forest disturbance (Sarbu, Janauer, Profft, Kaligarič, & Doroftei, 2014). Regarding significantly lower levels of temporal dissimilarity of avian communities in heterogeneous landscapes, it is not surprising because land-use richness promotes greater habitat stability and is more suitable for species (Tews et al., 2004). However, land-use richness was not a significant predictor for delta bird species richness. We speculate that the lower bird species richness in 2014/2015 in the mixed environments is linked to the loss of specialist species since mixed environments consist of different types of land-uses which should provide more heterogeneity and be more suitable for generalists (Devictor et al., 2008) instead of specialists species, which require specific habitats for feeding, breeding and nesting (Julliard et al., 2006).

Furthermore, Reif et al. (2013) reported a trend toward less habitat-specialised bird species in Czechia from 1982 to 2004. This declining trend of specialist species, described as the homogenisation of communities, has been recorded across Europe in different types of environments (Morelli et al., 2016). Nevertheless, we cannot state this with certainty since our study did not focus on a species level but on a community level.

A possible mechanism behind higher delta bird species richness (Fig. 5) and higher levels of dissimilarity (Table 2) in hills and mountains is the altitudinal range shift of central European bird species driven by climate change (Reif & Flousek, 2012). A similar pattern has also been recorded in birds in other countries, in the USA (Kirchman & Van Keuren, 2017) and Spanish mountain ranges (Tellería, 2020), as well as in other taxa, e.g. butterflies (Konvicka, Maradova, Benes, Fric, & Kepka, 2003). At the same time, some studies show a decrease in high-altitude bird species in northern Europe (Lehikoinen et al., 2014) and central European mountain ranges due to climate change and limited space at higher altitudes (Flousek, Telenský, Hanzelka, & Reif, 2015). These declines of high-altitude species and increases of low-altitude species together with their spread toward high elevations may facilitate the temporal turnover of bird communities in hills and mountains we observe in the data.

Ten years after the change in management strategies is a sufficient amount of time for visible population changes (Pellissier et al., 2019). Our study has the advantage of analysing the avian communities right after implementing SPAs in Czechia as part of Natura 2000. Although we cannot disaggregate the effect of Natura 2000 implementation from the overall effect of protected areas, we suggest protected areas are mitigating the current harmful effects of landscape changes on biodiversity, such as habitat degradation and homogenisation (Geldmann et al.,

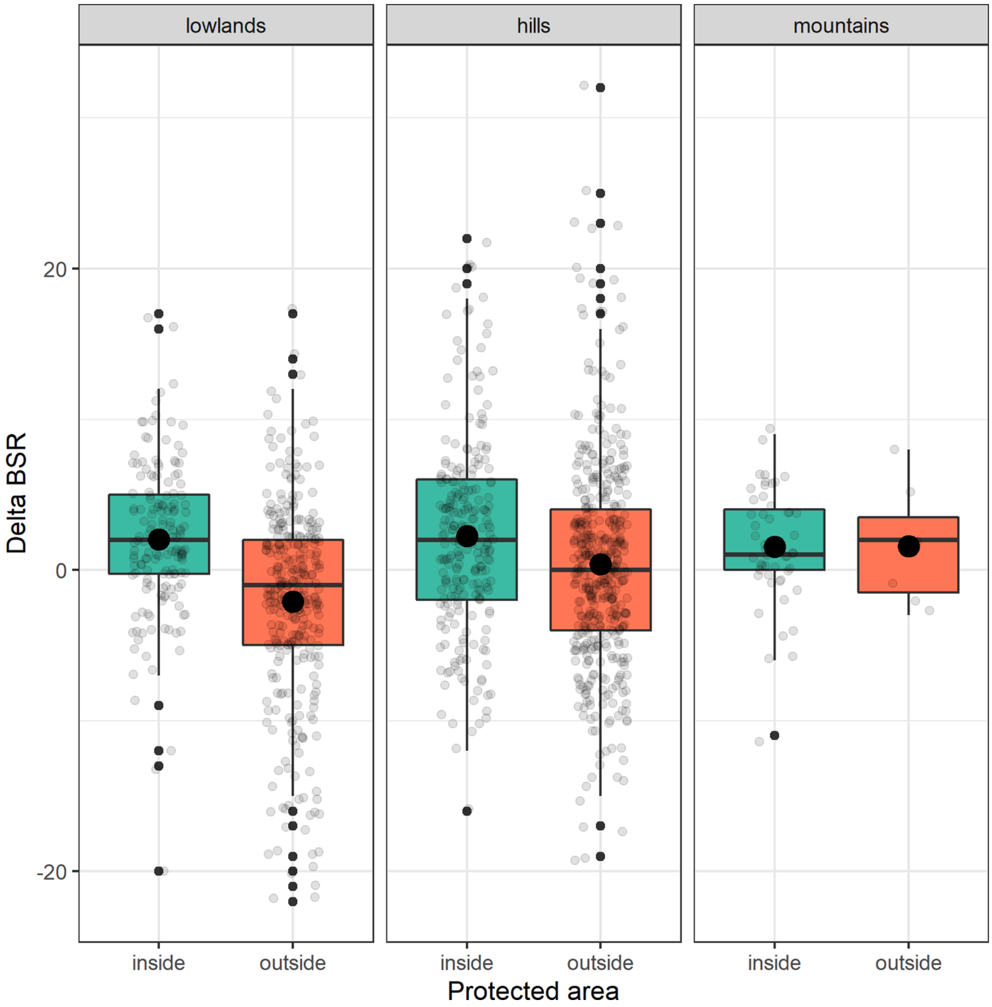

Fig. 5. Temporal changes in avian community between 2005/2006 and 2014/2015, measured as “delta bird species richness” (delta BSR) in relation to altitudinal zones inside (lowlands, n = 156; hills, n = 235; mountains, n = 50) and outside (lowlands, n = 319; hills, n = 442; mountains, n = 7) protected areas in Czechia.

2013). Moreover, our study assumes that bird species benefit from the ‘umbrella’ effect of the protected areas (Van Der Sluis et al., 2016), i.e., protected areas minimise the harmful effects on species even for which they were not designated for. Although we explained the observed temporal changes by the possible effect of the implementation of Natura 2000 as a conservation tool, land-use changes, and differences in communities across altitudinal zones, climatic data could provide more insight into the temporal changes of avian communities.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2022.126222.

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Annex 2. How are Natura 2000 protected areas covering different components of avian diversity in Spain?

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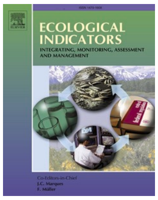

Original Articles

How are Natura 2000 protected areas covering different components of avian diversity in Spain?

Federico Morelli [a,b,*], Yanina Benedetti [a], Kristina Floigl [a], Juan Diego Ibáñez-Álamo [c]

[a] Czech University of Life Sciences Prague, Faculty of Environmental Sciences, Community Ecology & Conservation, Kamýcká 129, CZ-165 00 Prague 6, Czech Republic
[b] Institute of Biological Sciences, University of Zielona Góra, Prof. Szafrana St. 1, PL 65-16 Zielona Góra, Poland
[c] Department of Zoology, Faculty of Sciences, University of Granada, Granada, Spain

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ABSTRACT

Protected areas are a relevant conservation tool at our disposal, especially for developing management strategies of natural habitats. However, explicit tests at large spatial scales about its effectivity protecting different components of biodiversity are still rare. This study explored the spatial matching between the distribution of three components of avian diversity (taxonomic, functional, and phylogenetic metrics) and the network of Natura 2000 protected areas in Spain, the EU country with the most extensive terrestrial coverage.

Overall, the spatial distribution of taxonomic, functional, and phylogenetic diversity was slightly spatially congruent, matching with protected areas. However, each avian diversity metric showed differences in the arrangement of spatial clusters, also regarding the environment type. Species richness was higher in forests while it was lower in orchards, mixed environments, and arable lands. Functional dispersion was higher in forest and arable lands, while it was lower in wetlands. In contrast, the highest phylogenetic diversity was associated with wetlands and water bodies, with shrublands showing the lowest levels for this metric.

All three avian diversity metrics were overall higher within than outside the Natura 2000 network. The species richness was higher in areas simultaneously protected by the Habitat and Birds Directives. Functional dispersion was higher in protected areas designed under the Birds Directive. Finally, the evolutionary uniqueness was well represented in all protected areas, although areas designed under Birds Directive showed the higher values for this metric. The presence of spatial mismatch among avian diversity components suggests the importance of considering taxonomic, functional, and evolutionary metrics simultaneously for a better spatial prioritisation in conservation planning.

1. Introduction

High demand for natural resources across Europe has led to important landscape changes, homogenisation of natural habitats, and an overall decline of European biodiversity (De Baan et al., 2013; Young et al., 2005). This trend highlighted the need for immediate and effective measures to protect nature (Dirzo et al., 2014). For several decades, the presence of hotspots of biodiversity has been the main way to define protected areas' core area and boundaries, one of the most important conservation measures at our disposal (Barnard et al., 1998; Lascelles et al., 2012; Lombard, 1995). However, although several surrogates of biodiversity can be used to identify these biodiversity hotspots (Margules et al., 2002), these procedures have been mainly based on the total number of species (Bonn and Gaston, 2005). The use of species richness in macro-ecological studies is mainly due to the simplicity and cost-effectiveness balance of this metric, allowing quantifying a large amount of data in the species assemblages (Cadotte and Davies, 2010). Until now, protected areas usually have involved places characterised by a high number of species or holding a target proportion of species' geographic distributions (Fleishman et al., 2006; Maes et al., 2005) or areas under the Habitat Directive criteria or Birds Directive criteria. These criteria have been applied for designing protected areas in several countries like Spain. For example, bird species richness was used as the main criteria for identifying Important Bird Areas (IBAs; Carrascal and Lobo, 2003). Nevertheless, since species in a given community differ enormously among them, as well as in their particular vulnerabilities to threats, many studies suggest that conservation plans and management strategies need to evaluate different components of biodiversity such as

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

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taxonomic, functional, and phylogenetic diversity to increase their effectiveness (Benedetti et al., 2020; Jetz et al., 2014; Morelli et al., 2017; Wiens et al., 2008). Conservation strategies based only on taxonomic diversity could be inadequate to consider the ecological role of species and the functional contribution of each species to the community (Safi et al., 2013). The multi-component approach is particularly indicated in ecological assessments, since each component of biodiversity describes a different aspect of a given assemblage of species, as their links with the mechanisms and sources of variation of the ecosystem (Clark et al., 2012; Morelli et al., 2017; Petchey and Gaston, 2002; Tribot et al., 2016).

In line with this, the tools developed to mitigate the overall decline of biodiversity are many (de la Concha, 2005; Rodrigues et al., 2004; Venter et al., 2014). One of the most commonly applied approaches by conservationists is to identify areas with a high number of endemic species and habitat loss. These areas, identified as biodiversity hotspots (Myers et al., 2000), are regulated to achieve specific conservation objectives like the long-term protection of natural and cultural values (Mitchell et al., 2018). The European Union (EU) approach for the designation of protected areas follows two primary directives (the Birds Directive from 1979 and the Habitat Directive from 1992) that regulate the proposal of the Ecological Network Natura 2000 (Evans, 2012). However, a deep understanding of the effectiveness of the different types of protected areas to accomplish their main goal (i.e., conservation of biodiversity) is still missing (Fuller et al., 2010). In fact, there are several issues related to the management of protected areas, especially because such sites are a) constituted by overall complex social-ecological landscapes and b) often are managed through collaborative networks, involving different stakeholders and actors (Manolache et al., 2018).

From a conservation point of view, Spain is considered a high diversity country, part of the Mediterranean hotspot (CBD Secretariat, 2019; Mittermeier et al., 2005). Thus, protected areas with restricted use of natural resources and human impacts are needed to ameliorate the negative impact on biodiversity in this region (Gaüzère et al., 2016; Medail and Quezel, 1999). Spain is also the EU country with the most extensive terrestrial coverage by the Natura 2000 Network (150.000 km^2) (Múgica de la Guerra et al., 2019). Moreover, this Mediterranean country holds a high number of Important Bird Areas and plays a relevant role in this global network of protected areas for birds (Heath et al., 2000), and implicitly for biodiversity given the association between avian diversity and that of other taxa (Rodrigues et al., 2007; Sekercioglu, 2006). More than 45% of IBAs in Spain overlap with national protected areas, but only 15% of IBAs fell mostly within national protected areas (Evans and Heath, 2000). Furthermore, crops cover over 60% of IBAs in this Mediterranean country. Considering that agriculture has one of the highest impacts on bird species and their breeding sites, especially due to agricultural intensification (Butler et al., 2010; Evans and Heath, 2000), efficient, protected areas should be a key tool for mitigating the harmful effects of anthropogenic pressures that lead to a decline in different components of biodiversity (Hoffmann et al., 2018). But scientists are still debating if using protected areas as refugia to species from land-use change, climate change, and global warming is a successful strategy (Gaüzère et al., 2016). Thus, different studies demonstrated the importance of also considering functional or phylogenetic diversity, along with the number of species, for assessing the conservation status or potential threats of species assemblages (Morelli et al., 2017; Seymour et al., 2015). Therefore, it will be advisable to expand the current criteria for the identification and evaluation of protected areas, for example, by incorporating additional biodiversity components.

While the taxonomic diversity evaluates the number of species in each assemblage or community, the functional diversity measure is used to explore the relative weight of functional traits in the community, depending on the relative abundance of species characterised by such niche traits. The importance of functional diversity measures is associated with the fact that it can reflect processes underlying patterns in species assemblages as biotic homogenisation, the dominance of few species, or redundancy within the assemblage (Devictor et al., 2007; Morelli et al., 2016; Petchey and Gaston, 2002; Thompson et al., 2015). Finally, measures related to the phylogenetic diversity, for instance, the evolutionary distinctiveness, can assess the individual and overall degree of phylogenetic relatedness or uniqueness, which are fundamental for preserving evolutionary history or legacy through biodiversity (Frishkoff et al., 2014; Morelli et al., 2016).

This study aimed to evaluate the spatial congruence among three main components of avian diversity and assess the level of coverage of Spanish protected areas of such components of biodiversity, quantifying their effectiveness and identifying key areas that should be protected. Specifically, we compared the level of taxonomic, functional, and phylogenetic diversity of breeding bird species assemblages among the three types of Spanish protected areas (designed under Birds Directive, under Habitat Directive, and under both Directives), also considering the differences in bird diversity associated with different types of dominant environment and a degree of landscape heterogeneity.

2. Methods

2.1. Study area and bird species assemblages

The study area considered was the country of Spain. We used the data on breeding bird species occurrence obtained from the Spanish Atlas of Breeding Birds (Martí and Del Moral, 2003). This atlas compiled information on breeding birds during the reproductive season (April-June) of 18 years (1985–2002). It is based on the national census of breeding birds performed by the Spanish Ornithological Society (SEO/Birdlife; http://www.seo.org/) that follows standard methodologies to detect species reproduction (Martí and Del Moral, 2003). To alleviate temporal mismatches, we used distribution data of bird species of the most recent period available (2000–2002). Data used to consist of a geo-referenced dataset with the occurrence (presence/absence) for all bird species in each of the 5,390 10×10 km spatial units of a grid covering approximately 97% of the country's territory. In the selected period, every square was visited on average at least once, with a maximum of three visits. We did not find a significant association between the number of visits performed in each square and the total number of bird species detected, making the complete set of data homogeneous ($r^2 = 0.023$, $p > 0.05$).

This study considered the bird community composition as the species assemblage within each spatial unit (10×10 km square). We focused our investigation on breeding species because this period characterises the greater spatial stability of bird populations, facilitating the detection of individuals. This season is important for population recruitment (Bibby et al., 2000; Gregory et al., 2004).

2.2. Protected areas network and dominant environment

Data on protected area boundaries and type in Spain was obtained from the online Natura 2000 website (https://ec.europa.eu/environment/nature/natura2000/access_data/index_en.htm). We followed the classification of Natura 2000 sites provided in Appendix D for each Member State of the EU (European Environment Agency, 2019). The Appendix contains a sequential list of the relevant nature conservation designation types with statutory protection with their definition from the national/regional level. Natura 2000 areas were classified in three main categories, based on their designation under different European Directives:

- Protected areas according to the Birds Directive (79/409/EEC);
- Protected areas designed by the Habitat Directive (92/43/EEC);
- Protected areas under both Directives previously listed (Birds 79/409/EEC and Habitats 92/43/EEC).

The map of Spanish Natura 2000 areas was overlaid with a 10 × 10 km grid to match the bird breeding data (Fig. 1A). We estimated the percentage of overlap with each type of protected area for each square of the grid. All spatial data processing was completed using ArcMap (version 10.3.1) (ESRI, 2012). The coverages were transformed in percentage, and each 10 × 10 km square was classified as the main type of protected areas (PA) covered by using the following categories (see Fig. S1):

- Birds Directive: If the percentage of overlap with protected areas designed under the Birds Directive was higher than 60%;
- Habitat Directive: If the percentage of overlap with protected areas designed under the Habitat Directive was higher than 60%;
- Both Directives: If the percentage of overlap with protected areas designed under both Directives or overlapping both types of protected areas was higher than 60%;
- Other types of combination: If the percentage of overlap with protected areas designed under the Birds Directive, Habitat Directive, or both Directives were lower than 60%, but the overall percentage of overlap with all three protected area types was higher than 20%;
- <20% PA: If the total percentage of areas designed under the Birds Directive, Habitat Directive, or both Directives was lower than 20%; and
- Non-PA: If the square does not overlap with protected areas of any kind.

The use of 60% as the threshold permits a better classification, reducing misleading classifications when too similar coverages characterise two different categories in the same spatial unit or square (e.g., A = 51% and B = 49%) (Benedetti et al., 2020; Morelli et al., 2013).

Additionally, each 10 × 10 km square was also classified in terms of its dominant environment. First, land cover data was extracted from the CORINE land-cover (CLC) vector map (European Environment Agency (EEA), Copernicus programme, 2018), derived from 25-m resolution satellite data. The CORINE for Spain is a national geo-referenced land-cover database based on satellite digital images for all the country (Bossard et al., 2000). Land-use categories taken from CLC were reclassified in larger groups to obtain eight land-use types (i.e., arable, orchard, shrubland, forest, grassland, urban, and wetland/water bodies). Finally, each square was classified in terms of the dominant environment. Sites were classified as arable, orchard, forest, or any other category when one of these land-use classes was > 60% (Morelli et al., 2013). Sampling sites with mixed compositions and no dominant environments (no land use category covering > 60% of the square) were classified as mixed habitats (Fig. 1B).

2.3. Community and diversity metrics of avian assemblages

We calculated three different measures of avian diversity for each species assemblage (10 × 10 Km squares). First, we used overall bird species richness (BSR) as a measure of taxonomic richness (Magurran, 2004). Species richness was calculated as the total number of bird species recorded in each 10 × 10 km square.

$$BSR = S = Number\ of\ species$$

Second, we used functional dispersion as a species-trait approach focused on functional aspects of species assemblages. Functional diversity measures the range, abundance, and distribution of species traits such as body mass, feeding, and breeding characteristics, making it possible to link species diversity with ecosystem function (Laureto et al., 2015; Ricotta and Moretti, 2011; Villéger et al., 2008).

$$FDis = \frac{\sum a_j z_j}{\sum a_j}$$

where aj is the abundance of species j and z_j is the distance of species j to the weighted centroid **c**. The vector **c** is the weighted centroid in the i-dimensional space when considering the n species, and this value is weighted by the species relative abundances. More details in Laliberté and Legendre (2010).

In this study, we used the functional dispersion (FDis) (Mason et al., 2013) of bird communities. The FDis is the mean distance in the multidimensional trait space of individual species to the centroid of all species in the community (Laliberté and Legendre, 2010). A benefit of this index is related to the fact that FDis is fully independent of species richness and not too sensitive to outliers (Gerisch et al., 2012). Here, we calculated FDis using variables that describe niche traits of bird species related to feeding and breeding ecology (Pearman et al., 2014). The trait table consists of 52 binomial variables (scored as either 0 or 1) classified in (a) food types (13 variables), (b) behaviour used for acquiring food (9 variables), (c) substrate from which food is taken (9 variables), (d) period of the day of active foraging (3 variables), and nesting habitats (18 variables) (Pearman et al., 2014). The FDis was calculated using the

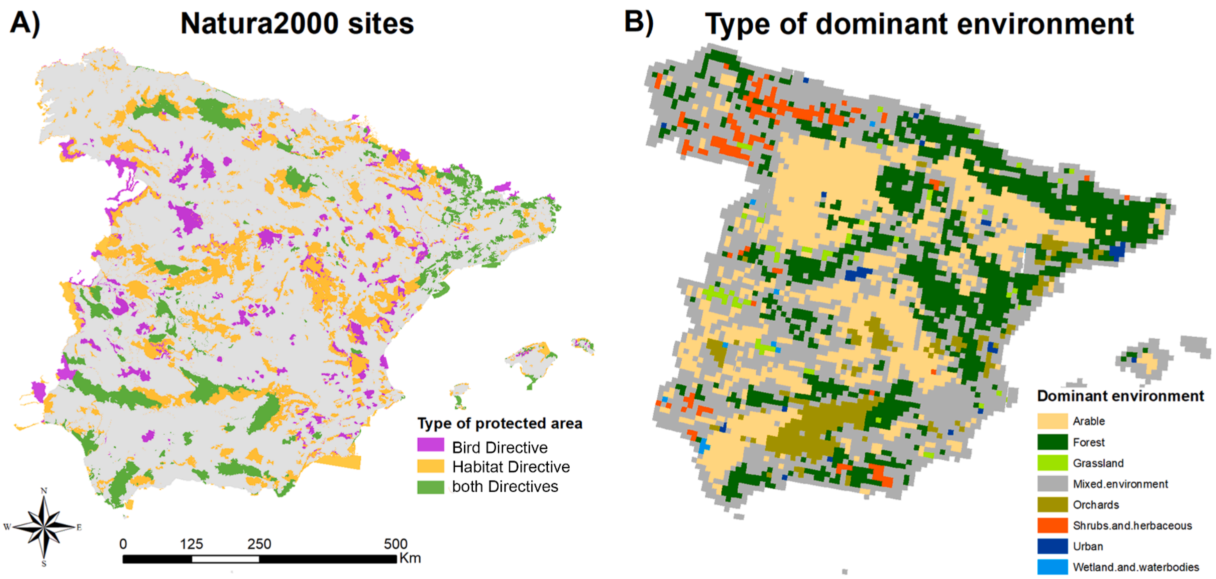

Fig. 1. Types of Natura 2000 areas, based on the category of designation (Birds Directive, Habitat Directive, both Directives) (A) and main types of dominant environments (B) in Spain. The spatial units used for mapping are 10 × 10 km squares (total number of squares 5,390).

'FD' package for R (Laliberté et al., 2015).

Third, we used the community evolutionary distinctiveness (CED) as a measure of the evolutionary uniqueness of the species assemblages. CED is a community metric based on the 'Evolutionary Distinctiveness' (ED) score (Isaac et al., 2007) and related to the avian phylogenetic diversity. The phylogenetic diversity is estimated using the sum of the branch length of the species present in the assemblage (Faith, 1992). The ED score for each bird species is calculated, dividing the total phylogenetic diversity of a clade by its members (EDGE of Existence, 2015). The CED is calculated as the average ED score in a given community or assemblage (Morelli et al., 2016; Tucker et al., 2017).

$$CED = \frac{\sum EDscores}{Number\ of\ species}$$

2.4. Statistical analyses

The explicit spatial congruence among BSR, FDis, and CED was tested by applying different Mantel tests (Legendre and Fortin, 2010; Mantel, 1967). Mantel test compares matrices with distances based on the differences in the values of each variable among sites. We run Monte Carlo permutations with 999 randomisations to test for the significance with the package 'vegan' for R (Oksanen et al., 2016). Additionally, we run generalised mixed models (GLMM) (Bates et al., 2014) to explore the direction of the associations between each type of diversity and community metric. The type of dominant environment was added as a random factor because we were not testing the interactions between diversity metrics and environments. We used the Box-Cox transformation method implemented in the package MASS for R (Venables and Ripley, 2002) to confirm the normality of all response variables (Triola, 2012).

To assess the differences in BSR, FDis and CED among different types of protected areas and non-protected areas in Spain, we run another series of GLMM. One avian community or diversity metric (BSR, FDis or CED) was modelled as the response variable in each model. In contrast, the type of protected area was modeled as an independent variable, and the type of dominant environment was added as a random factor. Additionally, since slight but significant spatial autocorrelation was detected for our response variables (BSR: $r_M = 0.071$ ($p < 0.001$); FDis: $r_M = 0.058$ ($p < 0.001$); CED: $r_M = 0.057$ ($p < 0.001$)), a term with Gaussian correlation structures was incorporated to all models (Dormann et al., 2007). All models were fitted by maximum likelihood, using the package "nlme" for R (Pinheiro et al., 2019).

All statistical tests were performed using the R software (R Development Core Team, 2019).

3. Results

3.1. Spatial distribution of avian diversity

Our study includes data from 5,390 10 × 10 km spatial units of a grid covering the whole territory of Spain. The data on breeding bird distributions used includes information from 330 different bird species. The five most frequently recorded bird species in Spain were: *Passer domesticus* (94.6%), *Turdus merula* (94.0%), *Carduelis carduelis* (93.7%), *Hirundo rustica* (93.3%), and *Serinus serinus* (93.2%) (Table S1). One hundred two species (31% of the total number of bird species) were rare, with an overall spatial distribution covering<1% of the total surface monitored (Table S1).

The spatial distribution of avian diversity in Spain showed clear differences depending on the diversity metric used (Fig. 2).

However, the spatially explicit correlation tests showed a significant spatial congruence between BSR and FDis ($r_M = 0.202$, $p < 0.001$), followed by BSR and CED ($r_M = 0.130$, $p < 0.001$), and FDis with CED ($r_M = 0.114$, $p < 0.001$). BSR was positively associated with FDis and CED, while the association between FDis and CED was statistically significant but slightly negative (Table S2).

Regarding the dominant environments, the values of diversity metrics of bird species assemblages were variable: The highest mean values of bird species richness were found in forests, while the lowest was associated with orchards, mixed environments, and arable lands (Table 1). The highest mean values of functional dispersion were found in forest and arable lands, while the lowest was related to wetlands and water bodies (Table 1). In contrast, the mean community evolutionary distinctiveness was highest in wetlands and water bodies while offered the lowest values associated with environments characterised by a dominant presence of shrubs and herbaceous vegetation (Table 1).

3.2. Avian diversity and protected areas

The mean values of bird species richness ranged from 68.2 in non-protected areas to 79.3 species in protected areas designed under both Directives (Table 1). The mean values of functional dispersion ranged from 8.03 in non-protected areas to 8.12 in areas with low protection coverage and 8.11 in protected areas designed under both Directives (Table 1). Finally, the mean values of community evolutionary distinctiveness ranged from 7.65 in non-protected areas to 7.93 in protected areas designed under the Birds Directive (Table 1). The percentage of 10 × 10 km squares intersected with each type of Natura 2000 protected areas in the different dominant habitats is shown in Table S3. 20% of Spanish squares were unprotected by the Natura 2000 network, although 36% of squares considered as protected have just a small (<20%) coverage of protected areas (Table S3).

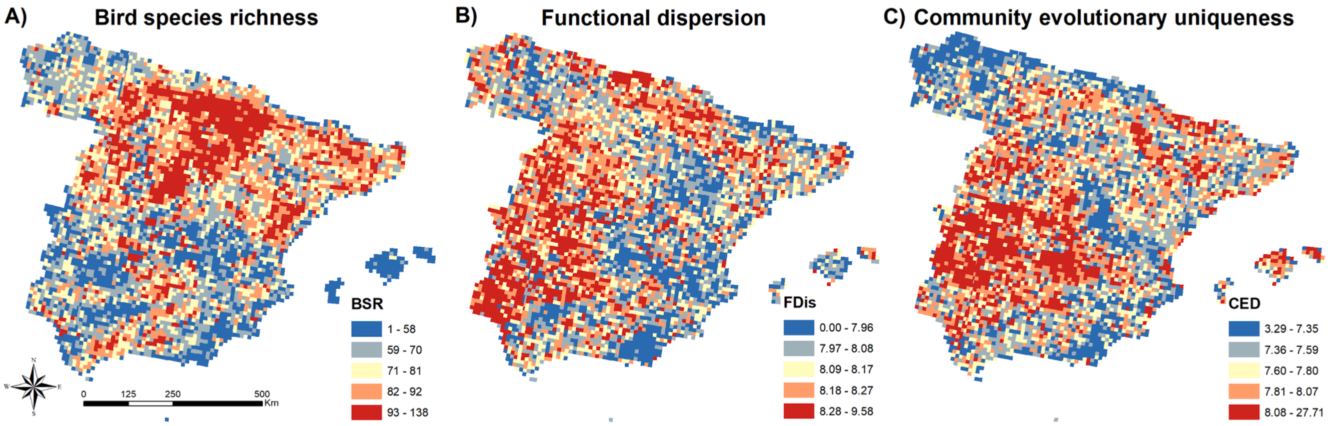

Fig. 2. Spatial distribution of avian diversity in Spain: A) the number of bird species, B) functional dispersion, and C) community evolutionary distinctiveness or uniqueness. The spatial units used for mapping consist of 5,390 cells of 10 × 10 km covering the Spanish territory.

Table 1
Mean, max, and min values of the three diversity and community metrics (bird species richness (BSR), functional dispersion (FDis), and community evolutionary distinctiveness (CED)) of bird species assemblages for each type of protected area and non-protected area, separately by the type of dominant environment, in whole Spain.

BSR																			
	Non-PA			**<20% PA**			**Birds Directive**			**Habitat Directive**			**Both Directives**			**Other type**			**Overall**
Type of environment	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
Arable	67.53	121	21	76.94	127	26	70.10	109	1	85.60	92	81	72.29	111	47	76.16	124	24	73.36
Forest	74.10	128	1	81.08	116	43	78.24	108	2	83.09	120	47	82.42	124	46	83.96	122	3	81.85
Grassland	75.57	90	64	76.17	106	6	75.25	98	53	78.00	98	64	73.19	104	41	74.88	138	1	75.06
Mixed environment	68.64	125	1	69.91	131	3	72.32	124	7	72.91	131	8	76.56	125	1	73.63	131	1	71.52
Orchards	62.92	108	28	73.93	113	38	52.00	52	52	69.67	71	67	85.33	91	82	75.97	105	46	69.66
Shrubs and herbaceous	70.63	96	47	72.00	121	33	–	–	–	70.23	94	22	79.15	120	5	74.39	104	54	74.20
Urban	68.93	89	47	79.50	118	42	–	–	–	–	–	–	83.00	83	83	88.00	96	80	75.67
Wetland and waterbodies	–	–	–	–	–	–	69.00	69	69	–	–	–	79.60	99	64	70.17	96	1	74.00
Overall	68.16	128	1	74.07	131	3	72.68	124	1	77.89	131	8	79.31	125	1	76.84	138	1	74.33
FDis																			
	Non-PA			<20% PA			Birds Directive			Habitat Directive			Both Directives			Other type			Overall
Type of environment	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
Arable	8.07	8.69	7.34	8.13	8.73	7.64	7.97	8.42	0.00	8.21	8.29	8.13	8.23	8.66	7.72	8.14	8.58	7.41	8.11
Forest	7.95	8.36	0.00	8.12	8.53	7.58	8.08	8.37	7.33	8.12	8.49	7.74	8.14	8.61	7.58	8.13	8.69	7.73	8.11
Grassland	8.27	8.38	8.17	8.18	8.90	7.64	8.15	8.31	8.01	7.93	8.19	7.75	8.11	8.33	7.57	7.68	8.37	0.00	8.03
Mixed environment	8.01	8.71	0.00	8.11	9.58	5.70	8.06	8.70	4.82	8.07	8.43	6.61	8.05	8.61	0.00	8.10	8.73	0.00	8.08
Orchards	8.02	8.54	7.49	8.11	8.56	7.52	8.07	8.07	8.07	8.33	8.49	8.17	8.11	8.19	8.06	8.12	8.36	7.78	8.07
Shrubs and herbaceous	8.17	8.49	7.88	8.10	8.55	7.69	–	–	–	8.05	8.60	7.63	8.05	8.42	7.74	8.07	8.48	7.74	8.08
Urban	8.11	8.37	7.88	8.18	8.44	7.83	–	–	–	–	–	–	8.32	8.32	8.32	8.30	8.40	8.20	8.16
Wetland and waterbodies	–	–	–	–	–	–	8.36	8.36	8.36	–	–	–	8.12	8.47	7.88	6.97	8.56	0.00	7.56
Overall	8.03	8.71	0.00	8.12	9.58	5.70	8.03	8.70	0.00	8.09	8.60	6.61	8.11	8.66	0.00	8.11	8.73	0.00	8.09
CED																			
	Non-PA			<20% PA			Birds Directive			Habitat Directive			Both Directives			Other type			Overall
Type of environment	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
Arable	7.75	9.04	6.18	7.83	9.16	6.46	8.10	12.67	7.14	8.35	8.91	8.04	8.11	8.94	7.28	7.95	9.11	6.54	7.85
Forest	7.47	8.32	6.56	7.56	8.69	6.58	7.57	8.25	4.82	7.67	8.40	6.38	7.67	8.78	6.56	7.64	8.71	5.60	7.62
Grassland	8.15	8.66	7.58	7.71	8.87	7.02	8.36	8.69	7.48	7.17	7.26	7.03	8.23	9.32	7.20	7.87	9.25	6.87	7.94
Mixed environment	7.54	9.22	3.33	7.63	11.12	3.29	7.90	9.63	6.36	7.74	11.57	5.75	7.92	27.71	6.45	7.72	9.80	4.38	7.67
Orchards	7.72	8.73	6.41	7.78	8.68	6.74	7.96	7.96	7.96	7.84	8.04	7.62	7.51	7.63	7.37	7.77	8.57	6.96	7.75
Shrubs and herbaceous	7.52	8.26	7.02	7.44	8.10	7.03	–	–	–	7.46	9.03	6.91	7.62	8.57	6.78	7.52	8.51	6.77	7.52
Urban	7.94	8.51	6.82	7.84	8.50	6.94	–	–	–	–	–	–	8.55	8.55	8.55	7.77	8.39	7.16	7.90
Wetland and waterbodies	–	–	–	–	–	–	8.57	8.57	8.57	–	–	–	8.04	8.31	7.84	9.12	14.24	7.65	8.63
Overall	7.65	9.22	3.33	7.68	11.12	3.29	7.93	12.67	4.82	7.69	11.57	5.75	7.80	27.71	6.45	7.74	14.24	4.38	7.71

Overall, bird species richness was significantly higher in protected areas designed under both Directives and another type of combination of protected areas than in any of the other categories. In contrast, species richness was lowest in non-protected areas (Table 2, Fig. 3). The only exception was found in arable landscapes, where we observed an increase of mean values of species richness in protected areas designed under the Habitat Directive (Fig. S2). The squares classified as “urban” were characterised by the total absence of protected areas coverage, or just a low coverage (<20%) (Fig. S2). The lowest values of functional dispersion of bird communities were associated with non-protected areas and protected areas designed under the Birds Directive (Table 2, Fig. 3). This pattern was relatively congruent through the different types of environments, except for grassland areas (Fig. S3). Within the protected areas network, the functional dispersion was relatively lower in protected areas designed under the Birds Directive, with a probable exception in grasslands and mixed environments (Fig. S3). The higher values were found, instead, in the Natura 2000 protected areas designed under both Directives. Finally, the evolutionary uniqueness of avian communities was significantly lower outside the network of Spanish protected areas than inside them (Table 2, Fig. 3). This difference was verified in most environments, with some exceptional cases characterised by a relatively high CED in non-protected areas associated with grasslands (Fig. S4). The highest values of community evolutionary distinctiveness were found in areas designed under the Birds Directive (Table 2, Fig. 3).

4. Discussion

4.1. Spatial distribution of avian diversity

The spatial distribution of the Spanish avian diversity showed clear differences depending on the diversity metric focused. This fact is important because it constitutes a further demonstration that more effective conservation planning at a large spatial scale needs to pay more attention to the different components behind the complex concept of biodiversity (Benedetti et al., 2020). For example, the spatial mismatch between taxonomic and functional diversity in the community of a given area can indicate particular community assembly rules, making necessary the simultaneous assessment of both measures for a better understanding of the ecosystem (Villéger et al., 2012). Additionally, the spatial mismatch can indicate areas that need special attention for different reasons: areas to be protected because of a high number of species or harbour some species more unique in terms of evolutionary legacy (Morelli et al., 2016). In our study, some protected areas were characterised by good protection of avian communities with relatively unique species from an evolutionary point of view (overall high CED). In contrast, the same areas were not equally important in terms of the total number of bird species. A good example is “Sierras de Alor Y Monte Longo”, a protected area located in the mountains to the southwest of the province of Badajoz, in the autonomous community of Extremadura. We highlighted this mismatch in example B, in Fig. S5.

Table 2

Results of generalised linear mixed models, accounting for variation in three components of avian diversity: bird species richness (BSR), functional dispersion (FDis), and community evolutionary distinctiveness (CED) concerning the type of Natura 2000 protected area in Spain. The type of dominant environment was added as a random factor in the modelling procedure (groups = 8). Additionally, to remove any spatial autocorrelation effect of dependent variables, a term with Gaussian correlation structures was incorporated in each model. Significant variables are indicated in bold.

BSR					
Variable	**Estimate**	**Std. error**	**DF**	**t-value**	**p-value**
Intercept	74.689	1.319	5377	56.584	0.000
Birds Directive	−2.728	1.736	5377	−1.572	0.116
Both Directives	**2.816**	**955**	5377	**2.946**	**0.003**
Habitat Directive	1.582	1.370	5377	1.154	0.248
Other type	**2.190**	**0.681**	5377	**3.214**	**0.001**
Non-PA	**−5.683**	**0.744**	5377	**−7.635**	**0.000**
FDis					
Intercept	8.117	0.012	5377	693.302	0.000
Birds Directive	**−0.097**	**0.036**	**5377**	**−2.657**	**0.008**
Both Directives	−0.006	0.019	5377	−0.331	0.741
Habitat Directive	−0.024	0.028	5377	−0.842	0.400
Other type	−0.009	0.014	5377	−0.609	0.542
Non-PA	**−0.087**	**0.016**	**5377**	**−5.592**	**0.000**
CED					
Intercept	7.777	0.092	5375	84.558	0.000
Birds Directive	**0.216**	**0.051**	**5375**	**4.252**	**0.000**
Both Directives	**0.204**	**0.028**	**5375**	**7.293**	**0.000**
Habitat Directive	**0.115**	**0.040**	**5375**	**2.857**	**0.004**
Other type	**0.097**	**0.019**	**5375**	**4.875**	**0.000**
Non-PA	**−0.074**	**0.022**	**5375**	**−3.389**	**0.000**

An important consideration related to this issue is that there is still no widely accepted single definition of “good biodiversity outcomes”. Despite the complex interaction of several biodiversity components, some ecologists have a positive output when one of these different diversity metrics is maximised (Pautasso and Dinetti, 2009). However, in cases like our study, data suggest that more complex definitions are needed in this respect. For example, the protection of a given area characterised by high species richness and simultaneously by high values of evolutionary distinctiveness can guarantee greater conservation of the phylogenetic heritage of avian assemblages. One potential case study from our results could be identified in the protected area ”Yesos de la Ribera Estellesa“, in the southwestern part of Navarra region, in the north of Spain (see example A in Fig. S5).

We found some spatial congruence between the taxonomic, functional, and evolutionary diversity of avian communities in Spain. However, the spatial patterns showed hotspots (areas characterised by high values) with clear regional differences among these three dimensions of avian community diversity. For example, we found higher values of species richness in avian communities mainly clustered in northern parts of the country (e.g. the regions of Castilla y León, La Rioja, Navarra and País Vasco), as well as in some parts of Valencia and Catalonia. This pattern was congruent with the results of previous studies (González-Taboada et al., 2007; Pascual et al., 2011) and perfectly matches with those performed with the same database (Carrascal and Lobo, 2003). Additionally, when focusing on the type of dominant environment, we found that avian communities of forests showed a higher number of species than in mixed environments and rural areas (arable land or orchards). Nevertheless, in this study, we did not focus on the level of discrimination of the different forest types due to the relatively coarse nature of the land use layer necessary to cover a national spatial scale study. A deeper analysis, including a more detailed classification of different forest types (from deciduous or perennial and discriminating in mixed forest and non-native ones), can reveal additional patterns of avian communities not captured with our analyses. For example, a study focused in NW Spain showed that non-native *Eucalyptus* forests, covering a large area of such regions, support bird communities characterised by a significantly lower number of species than bird communities from nearest native forests (Goded et al., 2019). Previously, Carrascal and Lobo already highlighted the important role of land use and land cover for the spatial distribution of avian species in Spain (Carrascal and Lobo, 2003). In a different Mediterranean country, a study investigating bird species assemblages of Central Italy showed a slightly higher number of species in cultivated areas than in forests (Morelli, 2015). However, these discrepancies could be related to specific differences between species assemblages in both countries. When comparing specifically forest avian communities in Spain and Italy, we can identify that avian communities of Spanish forests are richer than Italian ones, being shaped by the interactions between latitude and forest composition and structure (Charbonnier et al., 2016).

On the other hand, despite a general spatial congruence, we found that functional dispersion of avian communities showed a slightly

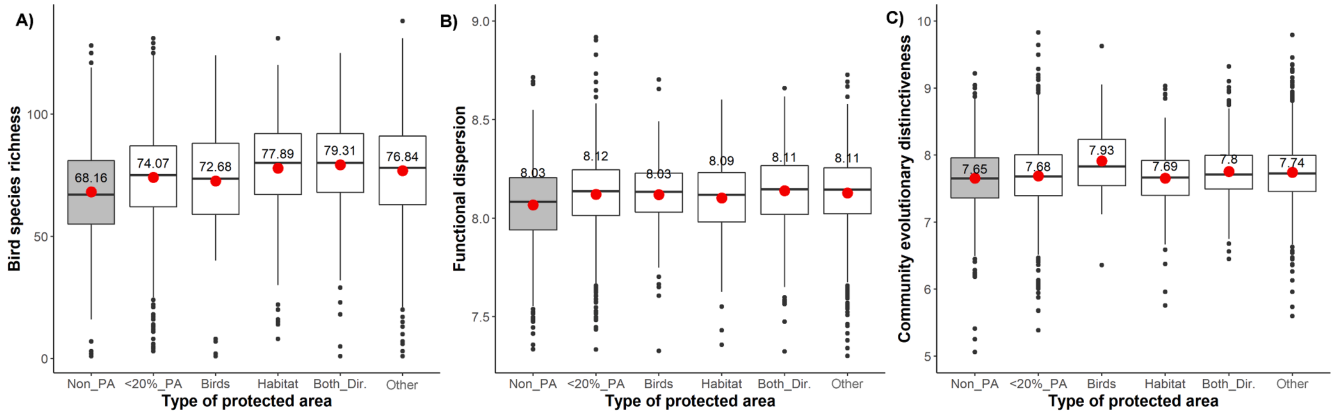

Fig. 3. Box plots of the number of bird species (A), functional dispersion in the avian species assemblage (B) and community evolutionary distinctiveness or uniqueness in each type of protected area (Birds Directive, Habitat Directive, both Directives, other combination types and < 20% covered by protected areas) or non-protected area (non-PA) in Spain. Box plots show medians (horizontal black lines), means (red circles), 95-percentiles and extreme values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

different spatial structure than that shown by the number of species: The highest values were less clustered than for species richness (see Fig. 2) and mainly concentrated in the Western part of the country (e.g., Extremadura, part of Andalusia, Castilla y León, and Cantabria), and mainly associated with forest and arable lands. Interestingly, the lowest mean values of functional dispersion were found for wetlands and waterbodies. This finding supports the concept that such types of environments (e.g., wetlands) are characterised by a more unified set of avian species in terms of ecological traits. For this reason, need special attention to mitigate conservation threats (https://cordis.europa.eu/article/id/182881-waterbird-conservation-status). The indices of functional diversity of a species assemblage represent an important aspect of the overall biodiversity, linked to different characteristics of the ecosystem, as functioning, productivity, and resilience, also has the potential to reveal community assembly rules and processes (Laliberté and Legendre, 2010; Mason et al., 2013). Functional dispersion is a facet of functional diversity that explicitly explores the dispersion of species in the trait space of the community, unaffected by species richness (Laliberté and Legendre, 2010). This measure quantifies the breadth of functional roles across species. Ecologists speculate that communities characterised by high functional dispersion display a greater functional dissimilarity. Thus, such communities are potentially more resilient since offering a broader range of responses to environmental stress (Cooke et al., 2019; Elmqvist et al., 2003). Even if this statement still needs support from empirical studies, open the possibility that Spanish avian communities potentially more resilient against climate or land-use change do not correspond with those bird assemblages with higher species richness. Another interesting indication is the confirmation that diversity indices *per se* are not a sufficient tool to assess the value for the conservation of a given area several times. For example, few species well adapted to wetlands and water bodies increase the need for conservation measures, despite the relatively low species richness and functional dispersions of such communities.

Finally, the evolutionary legacy of avian communities followed a spatial pattern more similar to the functional dispersion (although slightly more clustered) than to species richness. Initially, this could be interpreted as a positive indication that, in Spain, granting protection in certain areas could guarantee bird communities more resilient against global change threats while promoting the conservation of more unique evolutionary traits. The importance of the evolutionary legacy of communities is based on the presence of evolutionarily distinct species (e.g., with high ED score), birds that can display relict characters that are more isolated in the phylogenetic tree of life (Bennett and Owens, 2002; Redding et al., 2010). The great impact on conservation due to the loss of a unique evolutionary species is related to the fact that such loss cannot be easily compensated by introducing a different species (Lai et al., 2012). The current conservation strategies are increasingly stressing the benefits of considering species characterised by high values of ED score (Morelli and Møller, 2018; Redding et al., 2015). From this point of view, our results also support the use of initiatives considering the different dimensions or facets of biodiversity to better focus future conservation strategies.

4.2. Protected areas and avian biodiversity

There are different types of protected areas in Spain, with different regulations and management strategies (Múgica de la Guerra et al., 2019). The more effective type for conserving biodiversity are probably those characterised by more stringent regulations, in some cases even restricting several anthropic activities (Rodriguez-Rodriguez and Lopez, 2018). However, the spatial mismatch among three different components of avian diversity highlighted in our findings suggests that any set of conservation measures applied at a large spatial scale in the Iberian Peninsula need to explicitly pay attention to such spatial differences to maximise its protection capacities. This is mainly because associations among diversity metrics of avian communities change across different types of environments (Morelli et al., 2018).

Our findings underline the need to re-check the priorities regarding protected areas, as the majority have been created using taxonomic diversity criteria. Another study, centred mainly on the species richness and information about the conservation status of single species, suggested that the efficiency of protection strategies strongly depends on the type of data used or available (Carrascal and Lobo, 2003). We found that the Natura 2000 network offers a differential capacity to cover each diversity metric characterising Spanish avian communities. The ecological performance of protected areas was relatively good, in general correctly covering the overall Spanish avian diversity. However, the areas covering avian communities with a higher number of species are protected areas designed under both (Birds and Habitat) Directives or areas where the Birds and Habitat Directives are overlapped (European Environment Agency, 2019). This pattern is relatively constant across the different types of Spanish environments or habitats. Still, in arable lands, the protected areas designated under the Habitat Directive harbour richer avian communities than other types of protected areas. This fact is interesting, especially considering that the areas designed under the Habitat Directive are not directly focused on the occurrence of bird species. Additionally, is important to note that the number of species in avian communities in Spain seems to be lower outside the Natura 2000 network of protected areas, independently from the type of environment.

Regarding the functional diversity of avian communities (e.g., functional dispersion), the pattern was slightly less clear, a result somehow expected. Even if the functional dispersion values were overall higher in most of the Natura 2000 network than in non-protected areas, we found that one of the most common protected area in Spain (designed under Birds Directive) is probably not covering adequately the areas characterised by higher community functional dispersion in the country, especially in rural and forest areas. In grasslands, the performance of protected areas to cover the functional dispersion of avian communities was also underrated, being this value slightly higher outside than inside the protected areas designed under the Habitat Directive (see Fig. S3).

Last but not least, in this study, we also explored the distribution of the evolutionary uniqueness of avian communities in Spain. We found that the community evolutionary distinctiveness was significantly higher within the network of Natura 2000 protected areas, independently from the type of dominant environment. This result is, after all, encouraging conservation. Several studies, mainly focused in urban environments, have shown the potential benefits of focusing on using a complementary conservation perspective over more traditional taxonomic diversity metrics, for example with the use of avian evolutionary uniqueness (Ibáñez-Álamo et al., 2017; Morelli et al., 2016; Sol et al., 2017). The measures of phylogenetic diversity or uniqueness were, in fact, previously proposed to play a role in the establishment of conservation priorities (EDGE of Existence, 2015; Isaac et al., 2007). Regarding the conservation of the phylogenetic heritage of avian species, we also provided evidence that the Spanish protected areas designed under both Directives are covering avian communities with the highest evolutionary distinctiveness. Our findings support the idea that the designation of the Natura 2000 protected areas in Spain (and possibly in other countries) covers relatively correctly those areas characterised by evolutionary, more unique avian communities.

Overall, our results confirm that protected areas are a cornerstone of regional strategies for conserving the overall biodiversity (Gaston et al., 2008), even considering different components of avian diversity (e.g., taxonomic, functional, and evolutionary diversity). This is important also considering that each type of protected area is designed with different strategies, priorities, and by different teams of specialists, from national levels, or commonly agreed EU-wide criteria (Kukkala et al., 2016). However, our results highlighted that the overall congruence in spatial patterns of avian diversity at a national scale could also imply some local or regional mismatches that will require further attention in the near future. This fact also suggests that an approach considering the multifaceted nature of biodiversity should be the most suitable for conservation planning, providing a call of action for conservationists and policymakers. Additionally, the environment where the protected areas were established plays a role in their relative efficiency in protecting each dimension of avian diversity. Therefore, this factor should also be considered in the management and design of present and future protected areas.

Among some criticisms regarding our study, we can highlight two: a) The possibility to use different approaches to assess the avian diversity and b) a temporal discrepancy between the two layers of information crossed in this study (distribution of breeding birds and protected areas network in Spain). Regarding the potential use of different methods: Other approaches evaluating the spatial distribution of avian diversity could be focused on α-diversity (diversity within sampling sites). However, for a better understanding of biodiversity patterns at the landscape scale, the local scale comparisons could result inadequate. Some studies already suggested that macroecological patterns are not perfectly expressed by α and β diversity metrics (Chong et al., 2014; Hui and McGeoch, 2014). In our analyses, we preferred to perform multiple assessments of bird species assemblages by considering three main components of biodiversity (taxonomic, functional, and phylogenetic diversity) rather than performing paired *in-situ* comparisons. Regarding the temporal difference between the data source, even if we recognise a potential drawback in the analyses due to a temporal mismatch between the data on avian species distribution (2002) and the data of network of Spanish protected areas (2012), we retain that the main results obtained are reliable. First, the data on the distribution of breeding birds is the most complete currently available dataset at a relatively good spatial scale for all the country. Second, although some protected areas may have been established after 2002, we retain that the number and effect of such areas in the entire pool of data used for the modeling procedure covering the whole country could be considered neglectable (EUROPARC-España, 2019; Eurostat, 2021).

Despite the relevance of our general conclusions, our study suffers from a narrowed focus on breeding birds, then neglecting the importance of protected areas during migration and the wintering season. Further work focused on such periods is needed to better understand the effective value of protected areas in avian diversity through seasons. Finally, we hope that our findings will encourage further studies, which can apply spatial prioritisation, for example, highlighting the existence of single and multiple hotspots areas (Schröter and Remme, 2016) for each avian diversity or community measure and their importance for conservation.

CRediT authorship contribution statement

Federico Morelli: Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Yanina Benedetti:** Conceptualization, Data curation, Writing – original draft, Writing – review & editing. **Kristina Floigl:** Data curation, Writing – review & editing. **Juan Diego Ibáñez-Álamo:** Data curation, Writing – review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108452.

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Annex 3. Environmental Niche Modelling Predicts a Contraction in the Potential Distribution of Two Boreal Owl Species under Different Climate Scenarios

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animals

Article

Environmental Niche Modelling Predicts a Contraction in the Potential Distribution of Two Boreal Owl Species under Different Climate Scenarios

Kristina Cerman [1,*], Draženko Rajković [2], Biljana Topić [3], Goran Topić [3], Peter Shurulinkov [4], Tomaž Mihelič [5] and Juan D. Delgado [6]

[1] Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Suchdol, 165 00 Prague, Czech Republic
[2] Center for Biodiversity Research, Maksima Gorkog 40/3, 21000 Novi Sad, Serbia
[3] Ornithological Society ''Naše Ptice'', Semira Frašte 6/14, 71000 Sarajevo, Bosnia and Herzegovina
[4] National Museum of Natural History—Sofia, Bulgarian Academy of Sciences, 1 Tsar Osvoboditel Blvd., 1000 Sofia, Bulgaria
[5] DOPPS-BirdLife Slovenia, Tržaška Cesta 2, 1000 Ljubljana, Slovenia
[6] Department of Physical, Chemical and Natural Systems, Ecology Area, Faculty of Experimental Sciences, Universidad Pablo de Olavide, E-41013 Sevilla, Spain
* Correspondence: floigl@fzp.czu.cz

Simple Summary: Studying species distribution modelling in the face of climate change provides more insight into how endangered species are affected by these changes. Therefore, we studied two locally endangered owl species, the Boreal and Eurasian Pygmy Owl, in the Balkan Peninsula to better understand their current and future distribution. We aimed to perform species distribution modelling for these two targeted owl species in current climate and future predicted climate scenarios. We quantified highly suitable areas for both species currently and in future climate scenarios. Additionally, we looked at the size of the areas of future species' refugia where environmental factors might be suitable for the species. Results showed that the future highly suitable area for Boreal Owl shrunk compared to the current area in all climate scenarios; however, for Eurasian Pygmy Owl, the results did not follow such a clear trend. Our study is important from the species' conservation perspective and fills a knowledge gap about species distribution in the Balkan Peninsula.

Abstract: Studying current and future geographic distribution is essential for conserving endangered species such as the Boreal Owl and Eurasian Pygmy Owl. The main aim of this study was to determine the potential distribution of both species in the Balkan Peninsula by using spatial distribution models (SDMs) in MaxEnt. We used data from field surveys, the scientific and grey literature, and an online database. We considered the current time and two future periods, 2041–2060 and 2061–2080. For future periods, we included different climate scenarios (SSP 126, 245, 370, and 585) in studying the potential geographic distribution of both species. We identified two types of potential future refugia for species: in situ and ex situ. Our study shows the highly suitable area for the Boreal Owl increased during the 2041–2060 period compared with the current area in all scenarios, except in SSP 585. However, during the 2061–2080 period, the highly suitable areas contracted. For the Eurasian Pygmy Owl, highly suitable areas decreased during 2041–2060, but during the 2061–2080 period, it was larger than the current area. Our study is of importance for conservation and preserving areas of potential distribution and refugia for Boreal and Eurasian Pygmy Owls in the face of climate change.

Keywords: *Aegolius funereus*; Balkan Peninsula; climate change; *Glaucidium passerinum*; MaxEnt; species distribution modelling; suitability modelling; refugia

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1. Introduction

Biodiversity is a fundamental component of planet life-support systems, and human well-being depends on nature services, such as essential material goods, underpinning functions, and nonmaterial benefits [1–3]. However, biodiversity on our planet has been declining at an alarming rate in recent decades. This rate is predicted to be 100 to 1000 times bigger than natural background extinction rates [4–6] and is expected to continue at an increasing pace in the forthcoming decades [2–4].

Overall, five underlying key drivers cause biodiversity loss and species extinction via many pathways across different physical and temporal scales. These drivers include habitat loss, invasive alien species, overexploitation of natural resources, environmental pollution, and global climate change [7]. Among them, climate change is perceived as the major environmental issue of the 21st century and is anticipated to have vast negative consequences on the planet's biosphere [8]. The Intergovernmental Panel on Climate Change (IPCC) report predicts that global warming temperatures will likely reach 1.5 °C above preindustrial levels by 2040. Additionally, it is projected to grow by nearly 0.2 °C per decade [8]. Climate change strongly impacts biodiversity at various levels. It shifts species distribution [9–11] and migration phenology [12], affects population dynamics [13,14], changes community structure and composition [15], and influences the functioning of entire ecosystems [16,17].

Climate and species geographical distribution are causally related. Predicted global warming is expected to significantly impact the spatial distribution of biota worldwide. For instance, in environments closer to the Equator (i.e., tropics) or that are mountainous, species can be forced to shrink their distributions toward poles or move upslope to higher altitudes to escape warming temperatures and other unsuitable climatic conditions [18–20]. These changes in a species' distribution may jeopardise its persistence by reducing its range or fragmenting the population, leading to population size declines or risk of extinction [21–23]. Further, forecasts indicate that the population of habitat-specialised species is decreasing at a notably greater rate than habitat generalists [24,25]. Thus, relatively small biodiversity hotspots could be heavily threatened by climate change [26].

Therefore, over the last 30 years, scientists started studying species distribution modelling, also known as environmental (or ecological) niche modelling (ENM) [27–30]. This approach is based on mathematical algorithms that use data from presence/absence records and the environmental conditions at occurrence localities [29]. Specifically, modelling is applied but not restricted to predicting the potential geographical distribution [31,32] to recognise habitat suitability and priority areas for conservation [33–35], and, more recently, is used to study changes in geographic distribution concerning climate change [24,25,36]. One of the most used species distribution modelling approaches is the machine-learning algorithm MaxEnt (Maximum Entropy), American Museum of Natural History, New York, USA (for details, see [37–40]). MaxEnt is a favoured and widely applied tool because it demands only presence data, can utilise categorical as well as continuous variables, includes interactions between predictor variables, shows a satisfactory predictive performance, and generally outperforms other SDMs [41–43].

The Boreal (*Aegolius funereus*) and Eurasian Pygmy Owls (*Glaucidium passerinum*) are small, forest-dwelling avian predators belonging to the Siberian–Canadian faunal type [44,45]. Consequently, both species are confined to boreal climatic zones and high-mountain regions in the Palearctic (Eurasian Pygmy Owl) and Holarctic (Boreal Owl) realms. In Europe, they are almost sympatric inhabitants of the taiga belt in the northern parts of the continent. At the same time, several small, disjunct populations occur in high-mountain forests in the central and southern parts of the continent [44,45]. Across the European distribution range, both species are highly dependent on old growth (>80 years old), and primarily, coniferous forest stands, choosing dry and dead trees with cavities for breeding and food storage [45]. In Southern Europe, particularly on the Balkan Peninsula, both species prefer higher elevations, north-faced slopes, and medium-to-dense forests with a cold and humid climate [46–48]. Therefore, it can be assumed that Boreal and Eurasian Pygmy Owls are stenovalent habitat specialists with a narrow tolerance range and few possibilities of adaptation, which can only survive in the specific, above-mentioned environmental conditions. According to BirdLife International [49,50], there are less than ten thousand mature individuals of Boreal Owls (around 3% of the European population) and no more than six thousand mature individuals of Eurasian Pygmy Owls (about 2% of the European population) in the whole Balkan Peninsula. Knowledge about the spatial distribution range is limited, especially for the Eurasian Pygmy Owl, as well as information on population trends, except for a few countries where it is known that the numbers are decreasing (e.g., Serbia). Additionally, in almost all Balkan countries, both species are assessed as vulnerable or endangered with significant threats, such as forest exploitation and fragmentation, the development of ski resorts, and other human disturbances [51,52]. Further, due to global climate warming, the area comprising Norway spruce (*Picea abies*) in the central Balkan Peninsula, a primary habitat of both species, is expected to decrease, and the range will shift to higher altitudes [53]. Thus, the projected climate change may have a negative impact on the habitat suitability of both species, which may lose remarkable portions of their primary niche. Accordingly, determining the optimal forest habitat patches of both owl species is necessary to understand the role of topographic and climate factors in their potential habitat suitability under present and future climate scenarios.

The aims of this study were: (1) to define the potential current distribution through the development of an SDM and a set of environmental predictor variables; (2) to evaluate which environmental factor(s) influence spatial distribution; (3) to consider the potential impact of climate scenarios on the future distribution; and (4) to recognise potential refugial areas of Boreal and Eurasian Pygmy Owls in the Balkan Peninsula using MaxEnt modelling.

2. Materials and Methods

Our study area, the Balkan Peninsula, extends from Central Europe in the north to the Eastern Mediterranean region in the south, covering approximately 667,000 km^2, and is surrounded by the Adriatic, Ionian, Aegean, and Black Seas [54] (Figure 1a). Although belted by four seas, the Mediterranean climate is only present on the coast, with mountain ranges preventing warm air from penetrating into other parts of the peninsula [55]. Therefore, the rest of the peninsula is characterised by an alpine climate with strong altitudinal changes in precipitation and temperature, and by the continental climate in the river valleys and lowlands [56]. Due to the variety of climatic conditions, the Balkan Peninsula is one of Europe's endemism and biodiversity hotspots, as well as a glacial refuge for flora and fauna [57].

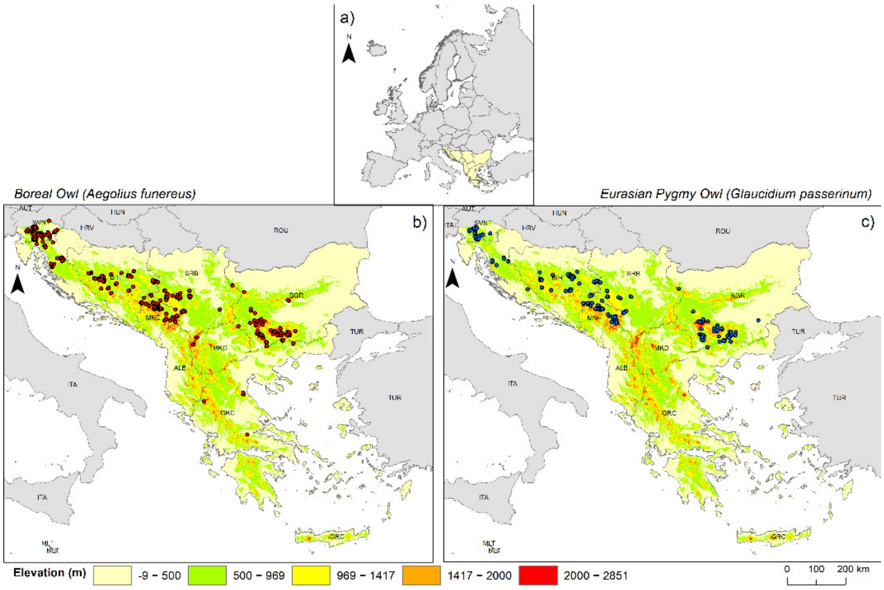

Figure 1. Study area (**a**) at a larger scale. Map of the study area with elevation of the Balkan Peninsula at a smaller scale with points where Boreal Owl (*Aegolius funereus*) (**b**) and Eurasian Pygmy Owl (*Glaucidium passerinum*) were present (**c**).

Regarding the vegetation cover, at an altitude of 0–700 m, forests comprise the mixed *Fagus* and *Carpinus* communities, with montane forest communities including mostly *Fagus* species [57]. At an altitude of 700–1700 m, the forest community comprises conifers such as *Abies*, *Picea*, and *Pinus*. Above this altitude is alpine vegetation with *Pinus*, *Juniperus*, and *Alnus* [57].

To compile the Boreal and Eurasian Pygmy Owls occurrence data (the geographic coordinates) from across their natural range in the Balkan Peninsula, we used three different sources: (1) an online database [58]; (2) the scientific and "grey" literature; and (3) records from targeted field surveys using GPS devices, which provided most data (>80%) used in this study. The IUCN Red List criteria for the size of the last three generations of a species were followed to provide biologically meaningful data. Therefore, the collected data related to the period from 2002 to 2020 (3 generations = 18 years) for the Boreal Owl and 2008–2020 (3 generations = 12 years) for the Eurasian Pygmy Owl were used. We derived 883 and 584 occurrence points of Boreal Eurasian Pygmy Owls, respectively. It is important to mention that differences in data collecting approaches were not expected to substantially impact the final model results because Maximum Entropy modelling is particularly well suited to handle all kinds of presence-only data [31].

After this initial step, we carefully cross-checked the data, deleted all duplicate records, and discarded data with obvious georeferencing errors. To avoid spatial autocorrelation in occurrence localities, we performed a filtering process of the rest of the occurrence data using the ArcGIS 10.7.1 software [59]. The spatial filter of occurrence localities was limited to 30 arc s between each other (ca. 1 × 1 km resolution at ground level), which is consistent with published data related to the territory density [47–60] and home range size [61,62] of both owl species. Thus, we left only one occurrence record within each grid cell of 1 × 1 km. Additionally, we used the Global Moran's coefficient for an additional recheck if there was a potential problem with spatial autocorrelation in the occurrence dataset [63]. This index represents the widely used multidimensional and multidirectional statistical tool for measuring spatial autocorrelation in ecological studies [64,65]. We employed the "Spatial Autocorrelation (Global Moran's I)" tool from ArcGIS (Esri, California, U.S.A.) software to calculate the Global Moran index using the nearest neighbour approach. We did not detect autocorrelated data in either the Boreal Owl (Moran's I = 0.047 $p = 0.573$) or the Eurasian Pygmy Owl (Moran's I = 0.189 $p = 0.748$). Finally, 439 and 235 precise occurrences of Boreal and Eurasian Pygmy Owls, respectively, were left (Table S1); these data were utilised to create the SDMs and the detailed distribution map (Figure 1b, c).

For modelling the current distribution of the species, we used recent bioclimatic variables, such as elevation, aspect and slope of the mountain, soil classification, snow cover, human footprint index, and land-use type. The sources of the environmental variables are available in Table S2.

Based on the published literature and the authors' assessment, climate and other predictor variables were selected according to their relevance and importance to owls' life cycles. For instance, it is generally known that most species, including Boreal and Eurasian Pygmy Owls, inhabit a specific bioclimatic niche which is predominantly regulated by main climatic factors such as temperature and precipitation [66,67]. In this case, both owl species across distributional ranges are associated with cold and humid boreal and high-mountain climate conditions [44,45]. Therefore, we decided to use all 19 different bioclimate variables from Global Climate Data–WorldClim version 2.1 [68] in the initial baseline model (present time, 1950–2000). These variables represent a crucial, ecologically meaningful, and the most applied set of high-resolution global climate layers in SDMs and related ecological modelling techniques [30,69]. In Southeast Europe, particularly in the Balkan Peninsula, Boreal and Eurasian Pygmy Owls, as postglacial relicts, inhabit high mountain areas, preferably above 1000 m a.s.l. Furthermore, they are cold-adapted forest-dwelling species that prefer north-facing, steep, often rocky slopes at higher altitudes covered with old-growth mixed and coniferous forests, usually grown in shallow soil [46–48,51,60,70]. In addition to bioclimatic variables, we included the digital elevation model

(DEM), slope gradient, aspect, soil type, and hill shade in the initial modelling in this study (Table S2). We did not include other potentially useful layers, such as land use or land cover, due to their high potential variability in time and space, making them unrealistic and irrelevant for modelling distribution patterns in future scenarios. To determine the future distribution of both owl species under contrasting climate scenarios, we used datasets of future climate predictions from Global Climate Data–WorldClim version 2.1 [68]. Four representatives of the Shared Socioeconomic Pathways (SSP126, SSP245, SSP370, and SSP585) ratified by the Intergovernmental Panel on Climate Change (IPCC) [8] were considered in modelling processes related to future climate scenarios and the habitat suitability distribution of both owl species. These SSPs are a part of the Coupled Model Intercomparison Project, Phase 6 (CMIP6) [8]. The four SSPs are defined by the predicted range of radiative forcing values [8]. Predicting suitable species distributions under climate change scenarios involved climate data for the next two periods: 2041–2060 and 2061–2080. All used layers were converted into a spatial resolution of 30 arc seconds (ca. 1 × 1 km resolution at ground level) and trimmed to the Balkan Peninsula shape using ArcGIS software.

We predicted the potential distribution of Boreal and Eurasian Pygmy Owls under different climate change scenarios by applying MaxEnt version 3.4.4. [38]. The MaxEnt program settings undoubtedly significantly influence model performance and prediction power [40]. Although the MaxEnt software can be successfully utilised for SDM purposes with the default settings [31], later studies have convincingly demonstrated that employing automatic features will not generally result in the best prediction model [71–73]. Therefore, respecting the calls for prudence and following general recommendations [73-74], we tried to achieve potentially the best combination of feature classes and a regularisation multiplier (β coefficient) to express the best fitting model adequately.

To model habitat suitability for each species (Table S3 and Table S4), we developed a comprehensive set of initial models with all 19 BioClim variables plus 5 topographic variables and a β coefficient changing from 0 to 5 in increments of 0.2, resulting in 26 models per owl species. Except for the β coefficient, other MaxEnt parameter settings were kept as the default. Tuning the β coefficient (regularisation multiplier) between 0 and 5 was a standard procedure that aimed to sufficiently reduce overfitting to reasonable levels [39,73]. For each species and each initial model, we used the sample-size-adjusted Akaike information criterion (AICc) [75,76] to determine the most appropriate variable combination and to tune model complexity [32,36]. We retained only the model with the lowest AICc from the initial set for each species, creating a baseline model. Moreover, we calculated the MaxEnt contribution scores for each environmental variable from each baseline model. Predictor variables indicating no remarkable effect on species occurrence with percent contribution scores ≤1% in the baseline model were eliminated. Then, the variable with the highest score was retained and added to the final variable set [77]. All other variables strongly correlated with the retained predictor variable at a pairwise Pearson correlation coefficient of $| r | > 0.70$ [36,78] were deleted. This process was replicated until all variables were switched to the baseline model set or discarded. Next, we checked the newly established set of the baseline model variables for multicollinearity with the help of a widely used diagnostic quotient: the variance inflation factor (VIF). All variables with a VIF score ≥6 [77,79] were eliminated from further processing, starting with the one with the highest VIF score. This process was repeated until all the remaining variables scored lower than 6. Altogether, 9 predictor variables for the Boreal Owl and 12 for the Eurasian Pygmy Owl were retained as inputs for MaxEnt modelling of Boreal and Eurasian Pygmy Owls in the Balkan Peninsula.

To reduce overfitting and simplify the interpretation [32,34], we only employed linear (L) and quadratic (Q) features and their combination (L + Q) in the finishing stage of the SDMs. This procedure resulted in generating three models per species. As in the previous steps, we retained the model with the lowest AICc to simulate the current and future distributions of the Boreal and Eurasian Pygmy Owls in the Balkan Peninsula. We set the maximum number of iterations to 1000 to allocate the models sufficient time to converge [35]. We applied “maximum training sensitivity plus specificity”, which represents a pretty satisfactory method for threshold selection in the case when only presence data are available[80]. The random test data were 25% of the sample data, and the training data were the remaining 75% of the sample data selected randomly. The habitat suitability curves of each predictor variable were calculated, as were the contributions of each predictor variable using the jack-knife test. All other MaxEnt parameter settings were kept as the default. We used the AUC (area under the ROC curve) to determine which models performed better than others. AUC values range from 0 to 1, with 0 being the lowest performance of the model and 1 being the highest performance of the model.

As metrics for quantifying the similarity among SDMs are important for testing patterns of niche evolution, we calculated the similarity statistic I [28]. It ranges from 0 (no overlap) to 1 (identical niche models). The mathematical formula is available in a study by Warren et al. [28].

All statistical tests were performed in RStudio [81].

After choosing the final models, we imported them into ArcGIS and divided habitat suitability into four levels according to the AUC values: unsuitable habitat (0–0.05), poorly suitable habitat (0.05–0.33), moderately suitable habitat (0.33–0.67), and highly suitable habitat (0.67–1). Various studies have different approaches in determining "highly suitable habitat" classification, where some are too strict (0.8–1) [82] and others are more accepting (0.6–1) [83–85]. Therefore, we decided to use a classification that would meet the requirements in the middle. According to these levels, we calculated the area of each species distribution under each climatic scenario and for each period, as well as an area of species distribution within each country.

We calculated areas of potential climate refugia for both species by looking at the highly suitable habitats in the current and future species distribution models. We followed the methodology of Brambilla et al. [32], where two types of refugia were identified: type 1 refugia are habitats suitable in both current and future conditions (in situ sites), and type 2 refugia are habitats that are not suitable in current conditions but provide suitable conditions in all future predictions (ex situ sites).

3. Results

The current species distribution prediction accuracy for Boreal and Eurasian Pygmy Owls was considered "excellent", where $AUC_{mean} = 0.91$ for both species (Table 1 and Table 2). Regarding the environmental variables for both species, bio5 (maximum temperatures of the warmest month) contributed the most to the MaxEnt models (74%). Interestingly, the Boreal Owl was absent in cells with maximum temperatures of the warmest month higher than 31 °C, whereas the Eurasian Pygmy Owl was absent in cells with maximum temperatures of the warmest month higher than 34 °C. The rest of the environmental variables all had less than a 10% contribution to the MaxEnt models. Regarding the current predicted distribution for the Boreal Owl, highly suitable areas cover 261 km^2, moderately suitable areas cover 447 km^2, and low suitable areas cover 1992 km^2 of the entire Balkan Peninsula (Table 3) (see Table S1 per country). For the Eurasian Pygmy Owl, highly suitable areas cover 233 km^2, moderately suitable areas cover 385 km^2, and low suitable areas cover 1271 km^2 of the entire Balkan Peninsula (Table 4) (see Table S2 per country). Both species had the largest areas of highly suitable habitats in Serbia and Bosnia and Herzegovina. Note that the alpine parts of Slovenia are excluded from the analysis since this area does not belong to the Balkan Peninsula.

Table 1. Mean AUC values (AUCmean) and standard deviation of the mean AUC values (AUCmeanSD) for the current and future MaxEnt models for Boreal Owl's distribution under different SSP scenarios.

Periods	**SSP**	**AUC_{mean}**	**$AUC_{mean}SD$**
Current		0.91	0.015
2041–2060	126	0.93	0.015
	245	0.89	0.021
	370	0.91	0.023
	585	0.89	0.024
2061–2080	126	0.88	0.023
	245	0.089	0.023
	370	0.86	0.026
	585	0.87	0.025

Table 2. Mean AUC values (AUCmean) and standard deviation of the mean AUC values (AUCmeanSD) for the current and future MaxEnt models for Eurasian Pygmy Owl's distribution under different SSP scenarios.

Periods	**SSP**	**AUC_{mean}**	**$AUC_{mean}SD$**
Current		0.91	0.025
2041–2060	126	0.87	0.037
	245	0.88	0.037
	370	0.92	0.016
	585	0.9	0.017
2061–2080	126	0.92	0.017
	245	0.94	0.009
	370	0.9	0.025
	585	0.92	0.019

Table 3. Extent of predicted three different categories of suitable habitats (km2) for Boreal Owl (*Aegolius funereus*) in current time, and in two periods: 2041-2060 and 2061-2080, in different climate scenarios (SSP 126, 245, 370, 585). Additionally, we calculated changes (%) from current time to future periods.

Years	**Scenarios**	**Predicted Area (km^2)**			**Changes in Area (%)**		
		Total poorly suitable habitat	Total moderately suitable habitat	Total highly suitable habitat	Total poorly suitable habitat	Total moderately suitable habitat	Total highly suitable habitat
Current	-	1192	447	261			
2041–2060	ssp 126	1355	440	276	13.67	−1.57	5.75
	ssp 245	1270	405	266	6.54	−9.40	1.92
	ssp 370	1266	452	280	6.21	1.12	7.28
	ssp 585	1107	386	222	-7.13	−13.65	−14.94
2061–2080	ssp 126	1255	397	249	5.29	−11.19	−4.60
	ssp 245	1248	399	248	4.70	−10.74	−4.98
	ssp 370	1128	391	247	-5.37	−12.53	−5.36
	ssp 585	1147	386	233	-3.78	−13.65	−10.73

Table 4. Extent of predicted three different categories of suitable habitats (km2) for Eurasian Pygmy Owl (*Glaucidium passerinum*) in current time, and in two periods: 2041-2060 and 2061-2080, in different climate scenarios (SSP 126, 245, 370, 585). Additionally, we calculated changes (%) from current time to future periods.

Years	**Scenarios**	**Predicted area (km2)**			**Changes in area (%)**		
		Total poorly suitable habitat	Total moderately suitable habitat	Total highly suitable habitat	Total poorly suitable habitat	Total moderately suitable habitat	Total highly suitable habitat
Current	-	1271	385	233	-	-	-
2041–2060	ssp 126	1279	338	214	0.63	−12.21	−8.15
	ssp 245	1357	359	212	6.77	−6.75	−9.01
	ssp 370	1641	404	206	29.11	4.94	−11.59
	ssp 585	1309	345	215	2.99	−10.39	−7.73
2061–2080	ssp 126	1588	399	238	24.94	3.64	2.15
	ssp 245	1641	454	238	29.11	17.92	2.15
	ssp 370	1451	391	232	14.16	1.56	−0.43
	ssp 585	1457	401	250	14.63	4.16	7.30

When looking at the future species distribution models for both species, all four scenarios (SSP 126, 245, 370, and 585) and both periods (2041–2060 and 2061–2080) were considered either “very good” or “excellent” (Table 1). The environmental variable for the Boreal Owl that contributed the most to the model was bio5 (maximum temperatures of the warmest month), with one exception for SSP 370 in 2041–2060, when bio9 contributed the most (69%). However, for the Eurasian Pygmy Owl, apart from bio5, elevation majorly contributed to the MaxEnt models. Regarding the area changes (Figures 2 and 3), specifically for the Boreal Owl, the highly suitable habitat in comparison to the current distribution was only positive, i.e., the area was larger than the current distribution, during the 2041–2060 period for SSP 126, 245, and 370. However, this was not true for SSP 585, where the changes were negative, i.e., the area was smaller than the current distribution. Furthermore, for the entire period of 2061–2080, we found changes to be negative, i.e., smaller than the current distribution. When looking at the area changes for the Eurasian Pygmy Owl, the highly suitable habitat in comparison to the current distribution was only negative during the 2041–2060 period for all scenarios. However, the 2061–2080 models predicted a positive change for all scenarios except for SSP 370.

Despite some changes in spatial distribution between the current and future predictions for both species, an ANOVA did not show statistically significant changes in the DEM (Boreal Owl p-value = 0.77, Eurasian Pygmy Owl *p*-value = 0.55).

Results obtained from the similarity statistic *I* showed that the Boreal Owl’s current niche highly overlapped with SSP 126 and 245 in the 2041–2060 period (0.926 and 0.991, respectively). However, when looking at the 2061–2080 period, the current species distribution overlapped highly with all except SSP 585 (0.719) (Table 5). Regarding the Eurasian Pygmy Owl, its current species niche moderately overlapped with all SSPs from the 2041–2060 period, but for the 2061–2080 period, its species niche highly overlapped with all SSPs (Table 5).

Table 5. Results of the similarity between species distribution models (SDMs) performed by calculating *I* statistics for Eurasian Pygmy Owl (*Glaucidium passerinum*) and Boreal Owl (*Aegolius funereus*). Comparison of current SDM with each SSP (126, 245, 370, 585) from each period (2041-2060, 2061-2080). *I* statistic ranges from 0-1, 0 being no similarity, and 1 being complete similarity of niche models.

Period	Climatic scenarios	Eurasian Pygmy Owl	Boreal Owl
		I statistic	I statistic
2041–2060	Current vs 126	0.857	0.926
	Current vs 245	0.825	0.991
	Current vs 370	0.706	0.882
	Current vs 585	0.872	0.442
2061–2080	Current vs 126	0.991	0.95
	Current vs 245	0.991	0.941
	Current vs 370	0.999	0.932
	Current vs 585	0.986	0.719

Our results show that type 1 refugia (in situ) of the Boreal Owl in the periods of 2041–2060 and 2061–2080 reduced its area among the different SSPs (Table 6) (Figure 4). Type 2 refugia (ex situ) followed the same pattern (Table 6). However, for the Eurasian Pygmy Owl, the area of the type 1 refugia in the 2041–2060 period was larger in SSP 126 and 585, and in 2061–2080 it was the largest in SSP 370 and 585 (Table 7). Furthermore, the Eurasian Pygmy Owl had a larger area of type 2 refugia in the 2041–2060 period in SSP 245 and 370, and in the 2061–2080 period, the largest in SSP 126 and 585 (Table 7).

Table 6. Extent of two types of refugia (km2) for Boreal Owl (*Aegolius funereus*). Area of type 1 refugium (in-situ refugium) and type 2 refugium (ex-situ refugium) for each period (2041-2060, 2061-2080) and each SSP (126, 245, 370, 585).

Refugium	**Period**	**SSP**	**Area (km²)**
type 1	2041–2060	126	232
		245	218
		370	221
		585	196
type 1	2061–2080	126	214
		245	206
		370	205
		585	207
type 2	2041–2060	126	45
		245	19
		370	14
		585	7
type 2	2061–2080	126	35
		245	23
		370	15
		585	9

Table 7. Extent of two types of refugia (km2) for Eurasian Pygmy Owl (*Glaucidium passerinum*). Area of type 1 refugium (in-situ refugium) and type 2 refugium (ex-situ refugium) for each period (2041-2060, 2061-2080) and each SSP (126, 245, 370, 585).

Refugium	**Period**	**SSP**	**Area (km^2)**
type 1	2040–2061	126	186
		245	168
		370	168
		585	180
type 1	2061–2080	126	184
		245	190
		370	203
		585	198
type 2	2040–2061	126	28
		245	44
		370	38
		585	35
type 2	2061–2080	126	54
		245	48
		370	29
		585	52

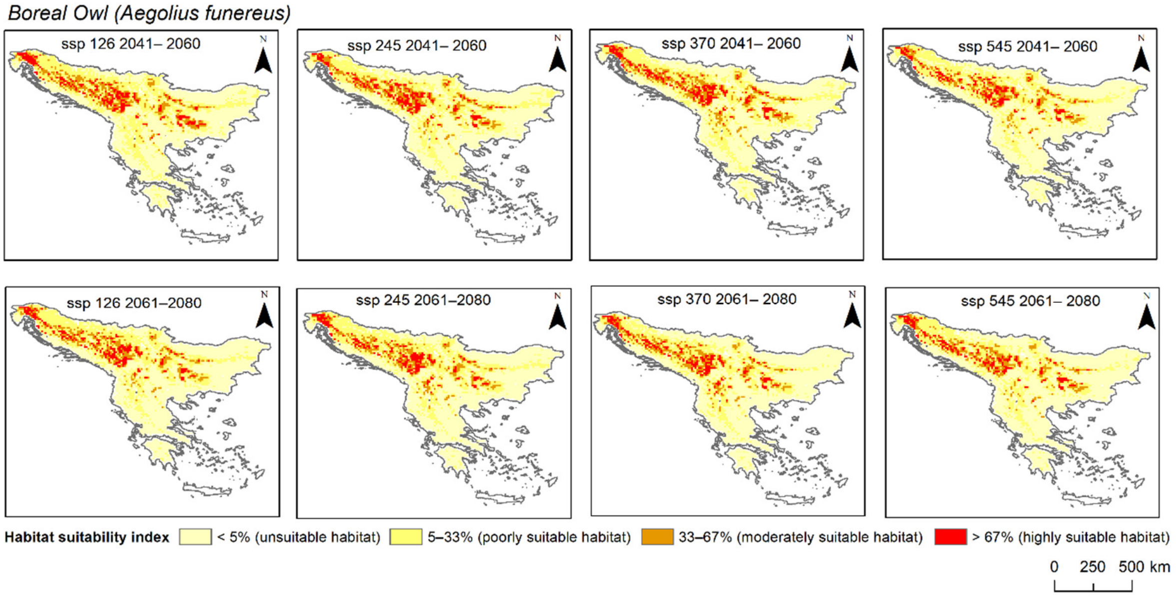

Figure 2. Predicted highly suitable habitat of Boreal Owl (*Aegolius funereus*) under projected future climate scenarios (SSP 126, 245, 370, 585) in two different periods: 2041–2060 and 2061–2080. Colour coding: beige = unsuitable habitat; light yellow = poorly suitable habitat; dark yellow = moderately suitable habitat; red = highly suitable habitat).

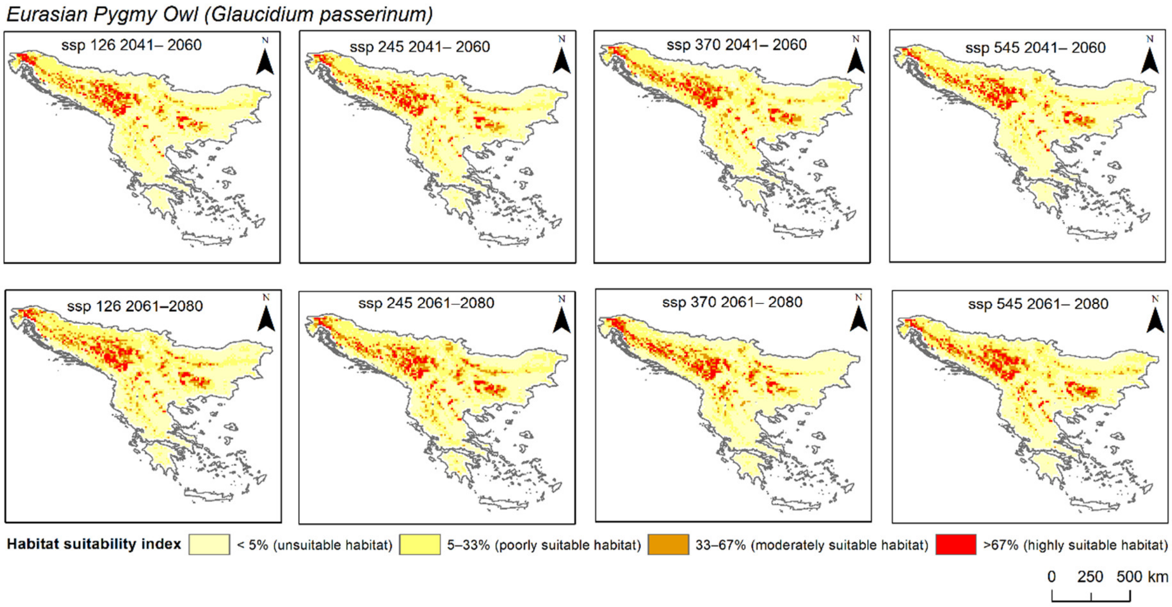

Figure 3. Predicted highly suitable habitat of Eurasian Pygmy Owl (*Glaucidium passerinum*) under projected future climate scenarios (SSP 126, 245, 370, 585) in two different periods: 2041–2060 and 2061–2080. Colour coding: beige = unsuitable habitat; light yellow = poorly suitable habitat; dark yellow = moderately suitable habitat; red = highly suitable habitat).

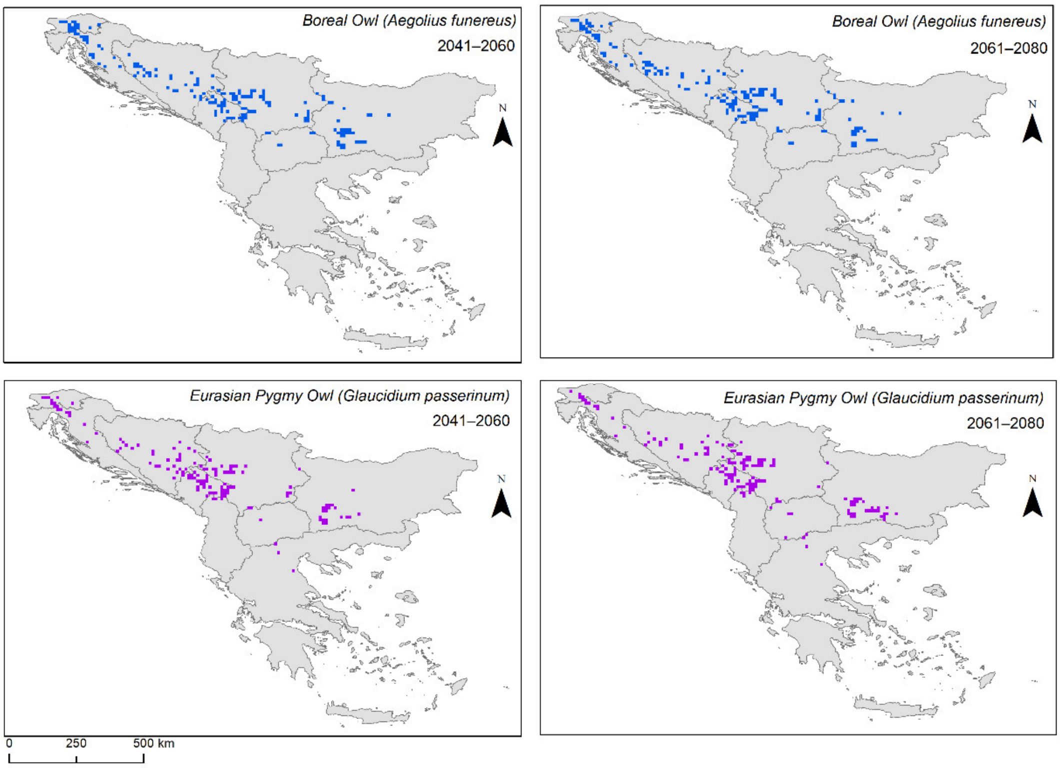

Figure 4. Type 1—in situ refugia for Boreal Owl (*Aegolius funereus*) and for Eurasian Pygmy Owl in the Balkan Peninsula in 2041–2060 and 2061–2080. Colour coding: grey = no refugia; blue = refugia for Boreal Owl; purple = refugia for Eurasian Pygmy Owl.

4. Discussion

Our results provide the first look at current and future species potential distributions of Boreal and Eurasian Pygmy Owls covering the entire Balkan Peninsula by using MaxEnt modelling. Additionally, our study provides more insight into the environmental and climate variables affecting current and future species distributions. Furthermore, we calculated species area changes and potential refugia at varying temporal scales for these two locally endangered boreal owl species in the face of climate change in the Balkan Peninsula. The outcomes of this study can be utilised to build future conservation strategies, and habitat restoration and management plans for these key, flagship predators of high-mountain habitats in the Balkan Peninsula.

The maximum temperature of the warmest month (bio5) represents the environmental variable that contributes the most to and notably shapes the Boreal Owl's and Eurasian Pygmy Owl's habitat suitability and spatial distribution. This is not very surprising since it is well known that high temperatures have a significant influence on boreal species, their distribution, and physiology. When looking at specific temperatures for each species in the current distributions, the Boreal Owl is more sensitive to higher temperatures than the Eurasian Pygmy Owl due to its absence in areas with higher temperatures than 31 °C. Similar results have been reported in a study from the Czech Republic, proving that Boreal owls prefer colder temperatures and higher altitudes [86], and which provides further evidence that species in southern populations, such as in the Balkan Peninsula, are a post-glacial relict. The next environmental variable that contributes the most to spatial distribution for the Eurasian Pygmy Owl was elevation. The species prefer higher altitudes, which contradicts the results from the study in the Czech Republic [86]. This is most probably because the Balkan Peninsula has a tree line at higher altitudes than the Czech Republic. Therefore, there is more forest area to inhabit. Altogether, these results suggest a high sensitivity of Boreal and Eurasian Pygmy Owl populations to maximum temperatures of the warmest month. Thus, any significant change in temperatures in the Balkan Peninsula and, probably, through a wider area might affect species potential distributions, as shown in other research for other avian species and geographical areas [87,88].

With global climate change, it is expected that some species will move close to the poles or high elevations [89,90] whereas other species might adapt to these changes [91]. However, in our study, when looking at the changes between current and future species potential distributions, we did not register statistically significant results. We can speculate that this is due to the tree line preventing species from moving to higher altitudes in the future and must consider the limiting factor for both species: higher temperatures at lower altitudes.

All projected distribution models, without exception, show narrow ecological adaptability in both owl species. When looking at the change in future highly suitable areas of the Boreal Owl, a positive change, i.e., the area increases in comparison to the current distribution, is overall present in the 2041–2060 period, except in SPP 585. This was expected, since SSP 585 is considered the worst-case climatic scenario in which CO_2 emissions rapidly increase until 2080, and then reach the peak at which the trend stabilises [8]. Furthermore, in the period of 2061–2080, only a negative change occurs, meaning the highly suitable area of the species distribution is reduced in comparison to the current species distribution. Regarding future highly suitable area changes of the Eurasian Pygmy Owl, the models showed that for the period of 2041–2060, the area would shrink in its size for each SSP. We can speculate that due to the increased temperatures caused by higher CO_2 emissions, both species' highly suitable areas will shrink, since, as it was previously discussed, the species are prone to avoid temperatures above 31 °C and 34 °C. Furthermore, a relatively new study carried out by researchers in the Bulgarian mountains showed that Boreal and Eurasian Pygmy Owls are avoiding inhabiting managed forests and young forests [70]. Even though Serbia and Bosnia and Herzegovina are facing urbanisation of mountainous areas with the development of ski slopes and touristic accommodations that require forest clear cuts [52], these countries still have the largest areas of highly suitable habitats for both species. Unfortunately, the combination of factors such as deforestation and increased temperatures might just be the reason for the loss of highly suitable habitats for these endangered species.

We calculated the type 1 refugia (in situ) of the Boreal Owl, the areas where the species is present currently and where it might be present in the future, under different climate scenarios. These areas are the most important for species conservation since they can enhance populations' resilience [92]. Our results showed that type 1 refugia would be increasingly contract with the different SSPs toward the worst-case scenario: SSP 585. This result was expected due to the increase in CO_2 emissions and higher temperatures. Furthermore, the ex situ refugia, type 2, where a species is not present currently but might be in the future, are important for the species' future redistribution [92]. Our models showed that the Boreal Owl's potential type 2 refugia would also contract with the different SSPs. However, both types of refugia of the Eurasian Pygmy Owl did not show such a clear trend along the SSPs. Even though our models showed that the future areas of both types of refugia are reducing, these areas are the key habitats for species protection and should be considered targets for conservation. Consequently, declaring these areas as protected areas and managing them accordingly could help support species' resilience to climate change.

With our study, we filled a knowledge gap regarding both researched species' current distribution in the Balkan Peninsula. Currently, there are several studies on Boreal and Eurasian Pygmy Owls' distributions in Serbia [52,93] and Bulgaria [48,51], with unpublished data from Bosnia and Herzegovina, Montenegro, and Croatia. However, little is known about the Boreal and Eurasian Pygmy Owls' population sizes and distributions in Albania and North Macedonia. Hence, our models of the current distribution of the species are beneficial for species mapping in these areas.

5. Conclusions

To safeguard Boreal and Eurasian Pygmy Owls, regular monitoring, habitat preservation, and sustainable management in the Balkan Peninsula are highly required. Special care must be paid to the core areas of both species, i.e., type 1 refugia which can be critical habitat patches for the future survival of both species. In addition, further detailed research is needed to determine how anthropogenic activities affect these two species' capacity to adapt to changing climatic circumstances.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ani12223226/s1, Table S1. Boreal (*Aegolius funereus*) and Eurasian Pygmy Owl (*Glaucidium passerinum*) occurrence coordinates obtained from (1) an online database [5], (2) scientific and grey literature and (3) records from targeted field surveys using GPS devices which includes most data (> 80%) used in this study.; Table S2. List of the six predictor variables, used for predicting future distribution of the Boreal and the Eurasian Pygmy Owl, with their sources form where they were obtained.; Table S3. Boreal Owl's current and future area (km^2) of highly suitable habitats in each Balkan country.; Table S4. Eurasian Pygmy Owl's current and future area (km^2) of highly suitable habitats in each Balkan country.

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Annex 4. Spatial Distribution and Habitat Overlap of Five Columbidae Species in the Czech Republic.

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animals

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Spatial Distribution and Habitat Overlap of Five *Columbidae* Species in the Czech Republic

Kristina Floigl [1,*], Yanina Benedetti [1], Jiří Reif [2,3,4] and Federico Morelli [1]

[1] Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Suchdol, 165 00 Prague, Czech Republic; ybenedetti73@gmail.com (Y.B.); fmorellius@gmail.com (F.M.)
[2] Institute for Environmental Studies, Faculty of Science, Charles University in Prague, Benatska 2, Prague 2, 128 01 Prague, Czech Republic; jirireif@natur.cuni.cz
[3] Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacky University Olomouc, 17. listopadu 50, 771 46 Olomouc, Czech Republic
[4] Czech Society for Ornithology, Na Bělidle 34, Praha 5, 150 00 Prague, Czech Republic
* Correspondence: floigl@fzp.czu.cz

Simple Summary: The spatial distribution of species and their utilisation of resources are essential for better understanding species ecology. Using data gathered by ornithologists in Czech Republic, we studied land use type utilisation of five pigeons and doves. Our study aimed to understand which species and type of land use are positively associated and whether the species are positively associated with land use heterogeneity. Additionally, we quantified the amount of land use type utilisation by each species and their spatial overlap in these land use types. We hypothesised that the species would mostly overlap in farmlands and urban areas. We found an almost complete overlap between the domestic pigeon (*Columba livia domestica)* and the Eurasian collared dove (*Streptopelia decaocto*), as well as between the common wood pigeon (*Columba palumbus*) and the European turtle dove (*Streptopelia turtur*). We confirmed our hypothesis that the species distribution not only overlapped in farmlands and urban areas, but also in forests. Our study provides insight into these common species distributions and habitat affinities.

Abstract: Habitat overlap occurs when two species co-exist in the same habitat and utilise the same resources. Using common bird monitoring data in Czech Republic from 2015 and 2016, we compared the affinities of five *Columbidae* species regarding land use types. Moreover, we analysed the effects of land use types and land use heterogeneity on five species distributions. The aim of the study was to quantify the habitat overlap of five *Columbidae* species regarding types of land use and land use heterogeneity. We predicted a high level of habitat overlap between most of the species and its occurrence in farmlands and urban areas. Our results confirmed the high habitat overlap of all five *Columbidae* species in farmlands. An almost complete overlap was recorded between *Columba livia domestica* and *Streptopelia decaocto*, as well as between *Columba palumbus* and *Streptopelia turtur*. Considering land use utilisation, *C. livia* and *S. decaocto* mainly utilised farmlands and urban areas. Furthermore, deciduous forests were utilised by *Columba oenas* and coniferous and mixed forests by *C. palumbus*. Finally, *S. turtur* mainly utilised grasslands and avoided urban areas. We conclude that *Columbidae* species overlap in spatial distributions, mostly in urban areas, forests, and farmlands. Our study provides a summary of these common species habitat affinities.

Keywords: *Columbidae*; Czech Republic; land use composition; habitat overlap; species distribution

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1. Introduction

Species ecological niche is a complex concept that reflects relationships to the environment, which are developed throughout the evolution of each species [1–3]. By adapting morphological, ecological, and physiological characters, species occupy ecological niches defined by environmental conditions and available resources. When two species co-exist in the same habitat, the habitat overlap occurs [4]. Under the conditions of habitat overlap, species compete for the common resources and this competition ultimately results in the local extinction of a less effective competitor [5] and/or in niche partitioning [6]. This process allows competing species to utilise the same resources in different ways, and thus promotes the co-existence of species [7].

Habitat loss may contribute to the increased habitat overlap in European landscapes due to agricultural practices and deforestation [8,9]. To avoid this overlap, species are colonising other suitable and available habitats, such as urban areas [10]. Colonisation of urban areas by birds has been occurring since the middle of the 20th century, and it is a process consisting of three stages: Arrival, adjustment, and spread [11]. At the same time, closely related species require a long time to develop interspecific differences [12]. Moreover, the number of species that have adapted to cities is still low since a small amount of species have developed the ecological and life history traits that lead them to be urban-tolerant species [13]. As a result, low interspecific competition and low species richness occur in cities, which are accompanied with high habitat overlap in urban areas.

The members of *Columbidae* family rank among the most common and widely distributed species in European landscapes. Their distribution overlaps in habitats, such as farmlands, urban areas, and natural forests [9]. To date, previous studies have analysed diet [14] and nest site overlap [15] in the *Columbidae* family. Additionally, several studies on *Streptopelia turtur* (Linnaeus, 1758) in the Mediterranean region focus on the effects of different types of landscape on the species [2–16]. However, to our knowledge, there are no records of studies concerning the distribution and habitat overlap of *Columbidae* species breeding in the Czech Republic, i.e., feral pigeon (*Columba livia forma domestica* Linnaeus, 1766), stock dove (*Columba oenas* Linnaeus, 1758), wood pigeon (*Columba palumbus* Linnaeus, 1758), Eurasian collared dove (*Streptopelia decaocto* Frivaldszky, 1838), and European turtle dove (*Streptopelia turtur*). According to a study on the performance of molecular phylogeny, *Columba* and *Streptopelia* species belong to different clades, i.e., *Columba* belong to the Old World clade and *Streptopelia* to a separate clade [17]. These birds may be an interesting group for studying habitat overlap due to the recent colonization of urban areas by some of these species [18,19]. For instance, in Finland, researchers have reported an increase in the abundance of *C. palumbus* in cities [20]. Furthermore, *C. palumbus* and *S. decaocto* are recognised as urban species and their populations are increasing in urban areas in Britain [21] and Baltic region [22]. In addition, according to specialisation traits in species tolerant to urbanisation, *C. livia* has the second highest relative urban tolerance score [13]. From the case of the Czech Republic, *S. turtur* is not considered an urban species due to its feeding behaviour, which requires open habitats, such as farmlands and grasslands [23]. *S. decaocto* is almost exclusively an urban species, and *C. palumbus* colonised urban areas recently in comparison to other European countries, where the colonisation process occurred earlier in the century [11].

Quantifying habitat overlap provides insight into species competition in specific habitats, thus allowing us to understand in which habitats competition is occurring and which types of land use require more conservation attention [2]. Here, we specifically focus on the role of landscape heterogeneity in the association with *Columbidae* species since it can provide more insight into species habitat type affinities. For instance, whether they are attracted to open space habitats with lower edge density, such as farmlands or to habitats with high edge density and fragments, such as urban areas. For this purpose, our study assesses whether two landscape heterogeneity metrics, land use richness and edge density, are significant predictors of *Columbidae* species distribution.

Moreover, studying the ecology of species, such as *C. oenas* and *S. turtur*, can provide insight for conservation strategies due to their potential to serve as umbrella species. Commonly, effective umbrella species should cover a large geographical area, and have high spatial and habitat overlap with co-occurring species [24,25]. For instance, *S. turtur* is a vulnerable species listed on the Annex II of the Birds Directive, that aims to allow for the hunting of species to be sustainable [26]. Therefore, the prohibition of hunting *S. turtur* during specific periods allows other farmland species to benefit from these measures, as well.

The main aim of our study is to quantify the habitat overlap of five species of the *Columbidae* family present in the Czech Republic regarding land use composition and land use heterogeneity. Within this goal, our objectives were to map the species, calculate the species habitat overlap index, assess the habitat selection, and determine the relationship of land use types and landscape heterogeneity with the occurrence of the following five species: *C. livia*, *C. oenas*, *C. palumbus*, *S. decaocto*, and *S. turtur*. We predicted a high level of habitat overlap among most of the species, and that the habitat overlap would occur in farmlands and urban areas [11] due to the species spatial distribution and the detected increasing number of *Columbidae* species in urban areas. Furthermore, regarding species phylogeny, we can predict two possible outcomes: (i) Species within the same clade will show a greater overlap than distantly related species from different clades due to the relatively short time since their divergence; (ii) closely related species from the same clade will show a smaller overlap due to the higher interspecific competition.

2. Materials and Methods

The data were collected at 118 study sites scattered in different land use types and altitudes throughout the Czech Republic within the Bird Breeding Monitoring Program in 2015 and 2016. The Program is conducted by voluntary ornithologists using point counts [27]. Each site is represented by a transect comprising approx. 20 sampling points located 300–500 m apart. In total, 2324 point counts were visited. Birds are visited twice per breeding season at each sampling point, to cover both early and late breeders. During one visit, birds detected both visually and acoustically are counted for 5 min at each sampling point. We considered only the counts within a 100-m radius around each sampling point.

In this study, we used the presence and absence of four Columbidae species (specifically, *C. livia*, *C. oenas*, *C. palumbus*, *S. decaocto*, and *S. turtur*) at the sampling points. Presence at sampling points was attributed when the species was observed at least once during the 2 years of observations, while absence was assumed when the species was absent in both survey years. For better visualisation of sampling points where each species was present and species richness per each sampling point, we mapped the sampling points using the Kernel density interpolation method from ArcGIS (Figures 1 and 2).

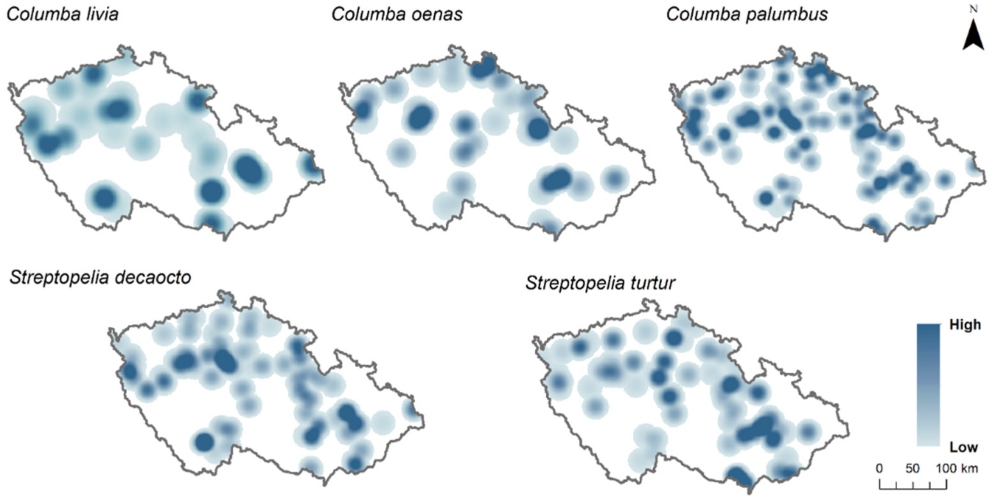

Figure 1. Five Columbidae species distribution in the Czech Republic with Kernel density interpolation. The darker blue colour represents a high density of points, where species were present during the survey; light blue colour represents a low density of points, where species were present during the survey; white areas are where census transects are missing. Distribution of five species: Feral pigeon (*Columba livia forma domestica*), stock dove (*Columba oenas*), wood pigeon (*Columba palumbus*), Eurasian collared dove (*Streptopelia decaocto*), and European turtle dove (*Streptopelia turtur*).

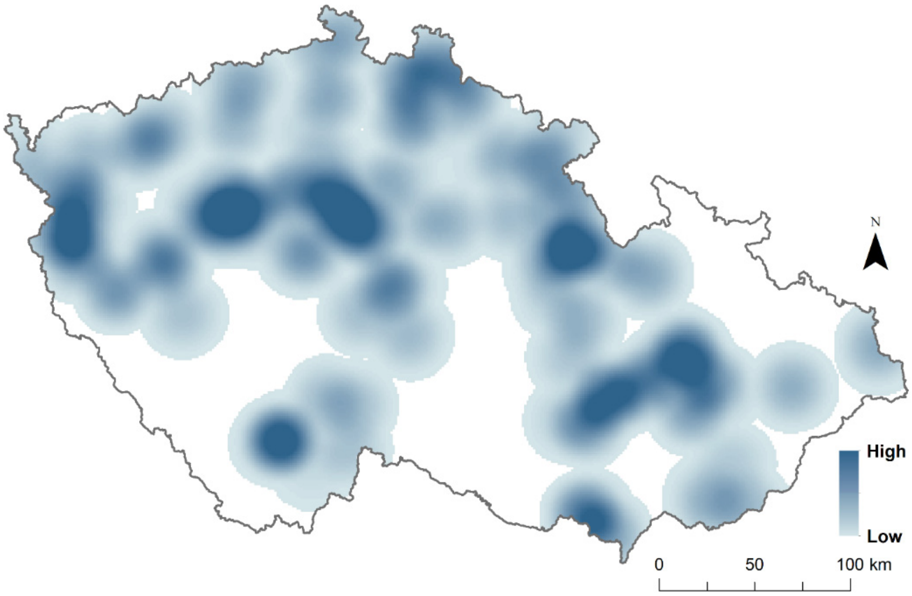

Figure 2. Species richness distribution of five *Columbidae* species in the Czech Republic with Kernel density interpolation. The darker blue colour represents higher species richness; light blue colour represents lower species richness; white areas are where census transects are missing. The included species are feral pigeon (*Columba livia forma domestica*), stock dove (*Columba oenas*), wood pigeon (*Columba palumbus*), Eurasian collared dove (*Streptopelia decaocto*), and European turtle dove (*Streptopelia turtur*).

The land use map of the study area was provided by the Nature Conservation Agency of the Czech Republic as the consolidated layer of ecosystems (CLE). CLE is based on a country-wide habitat mapping performed during the early 2000s and updated to 2018 [28]. We used ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA, USA: Environmental Systems Research Institute [29] to calculate land use composition around the 100-m radius of each point count. Land use composition consists of seven land use types: Deciduous, coniferous, and mixed forests, farmlands, grasslands, urban areas, and land use types, which were grouped into one category as "other", such as shrubs, quarries, rocks, and water. Furthermore, to quantify landscape heterogeneity, we calculated two landscape metrics: Land use richness, which is the number of different land use types per site [30], and edge density, which is the ratio between total lines or perimeters and total area of each site [31]. Both landscape metrics were calculated within the 100-m radius of each point count.

We compared the Columbidae species affinities regarding the land use types using the function "habitat overlap", from the "indicspecies" package in RStudio, which compares pairs of resource niches. The function returns the overlap index between each pair of species [32], using the amount of resource utilised by each species. The index value ranges from zero (no resources are shared by the two species) to one (all of the resources are shared).

To analyse the differences in utilisation of land use among the species, we used the habitat overlap module from the "EcoSimR" package in RStudio [33]. It allowed us to plot the resource utilisation matrix. The plot provides a visualisation of the observed utilisation matrix, the area of each circle is proportional to the utilisation of a land use type by each species. If there is no circle, the utilisation matrix is zero.

To analyse the effects of land use types, land use richness, and edge density on species distribution, we performed generalised linear models (GLM) [34] for each species. To account for the potential spatial autocorrelation (SAC) between sampling points, we applied a Mantel test [35]. The Mantel statistic (r_M) varies between −1 and +1. It evaluates the similarity between two matrices, first calculated as a geometric distance, and the second one with a geographical distance among the sampling sites [36]. To test for the significance on the Mantel test, we ran the Monte Carlo permutations with 999 randomisations [37].

No significant autocorrelation was detected in the dataset used for the analyses (Mantel test, 999 randomisations: $r_M = 0.09$, simulated $p > 0.05$). Furthermore, to assess the relationship between species richness and land use types, as well as between land use richness and edge density, we performed a separate GLM with Poisson distribution.

In the GLM species, presence and absence were used as a response variable assuming a binomial distribution. In addition, land use type (deciduous forest, coniferous forest, mixed forest, urban areas, farmlands, grasslands, etc.), land use richness, and edge density, were used as predictors. After building full models, i.e., the models containing a complete set of predictors, for each species, a test of variance inflation factor (VIF) was applied to check for potential multicollinearity issues among predictor variables, using the function "check_collinearity" from a "performance" package [38] for RStudio. Only variables with VIF < 6 were introduced in the final models [39].

All of the statistical tests were performed with RStudio: Integrated Development for R. RStudio, PBC: Boston, MA, USA [40].

3. Results

The habitat overlap analysis included a total of 2324 sampling points of presence and absence of five Columbidae species, seven different land use types, and two landscape metrics. The most widely distributed species of Columbidae in the Czech Republic was *C. palumbus*, with 62% (n = 1448) of occupied points, followed by *S. decaocto* with 21% (n = 499), *S. turtur* with 15% (n = 357), *C. oenas* with 8% (n = 191), and *C. livia* with 7% (n = 168) of the total occurrence in the country (Figure 1). In addition, no sampling point had all five species present, nine sampling points had four species present, 131 sampling points had three species present, 558 sampling points had two species present, and 1118 sampling points had one single species present (Figure 2).

The habitat overlap index based on land use composition at sampling points shows an almost complete habitat overlap between pairs of *C. livia* and *S. decaocto*, as well as between *C. palumbus* and *S. turtur*. On the contrary, the smallest habitat overlap was estimated between *C. livia* and *C. oenas*, as well as between *S. decaocto* and *C. oenas*. Furthermore, *C. oenas* had an 0.8 habitat overlap index with *S. turtur* and *C. palumbus* (Table 1). When looking at the mean habitat overlap, *C. palumbus* had the highest habitat overlap with the other Columbidae species, followed by *S. turtur*. On the contrary, *C. oenas* had the lowest mean habitat overlap (Table 1). According to the utilisation plot, mixed forests, farmlands, grasslands, and other land use types were equally used by all five species, except for *C. oenas*, which utilised farmlands less than the other species. In deciduous forests, mostly *C. oenas* was present, while in coniferous forests, in addition to *C. oenas*, *C. palumbus* and *S. turtur* were present. Urban areas were inhabited mainly by *C. livia* and *S. decaocto* (Figure 3).

Table 1. Habitat overlap among five *Columbidae* species (feral pigeon (*Columba livia forma domestica*), stock dove (*Columba oenas*), wood pigeon (*Columba palumbus*), Eurasian collared dove (*Streptopelia decaocto*), and European turtle dove (*Streptopelia turtur*)) was estimated as a similarity index based on land use composition and two landscape metrics at each site where the species were present. Value of one suggests that the species are completely sharing resources. Value of zero indicates that the species do not share any resources. Mean—mean habitat overlaps for each *Columbidae* species.

	C. livia	***C. oenas***	***C. palumbus***	***S. decaocto***	***S. turtur***	**Mean**
C. livia	1					0.659
C. oenas	0.391	1				0.627
C. palumbus	0.735	0.820	1			0.838
S. decaocto	0.988	0.472	0.808	1		0.755
S. turtur	0.664	0.825	0.990	0.752	1	0.799

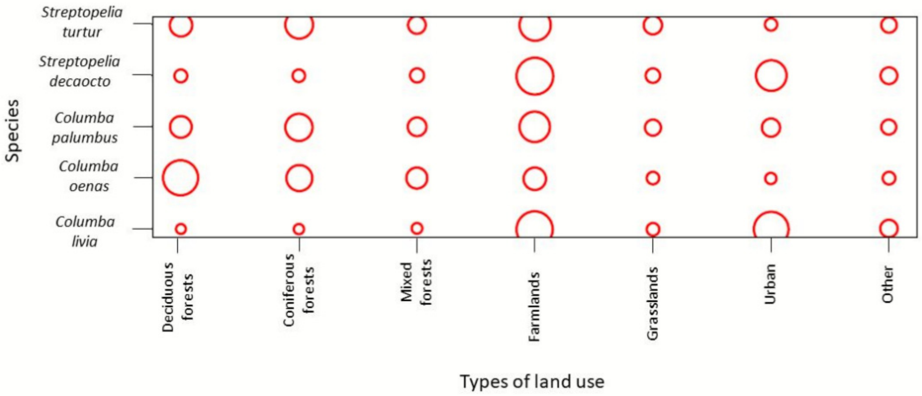

Figure 3. Habitat utilisation matrix based on land use composition around sampling points of five species from the family Columbidae in the Czech Republic. The figure provides a graphical portrayal of the observed utilisation matrix, and the increasing area of each circle is proportional to the increasing utilisation of each land use type by each species. If no circle is shown, the utilisation is zero. There are seven types of land use.

The presence of *C. livia* was negatively associated with deciduous, coniferous, and mixed forests, farmlands, grasslands, and other types of land use, and positively with edge density (Table 2). *C. oenas* showed negative associations with farmlands and urban areas, and positive associations with deciduous and mixed forests (Table 3). A model for *C. palumbus* showed only the positive associations—with coniferous and mixed forests (Table 4). *S. decaocto* was negatively associated with deciduous, coniferous, and mixed forests, farmlands, grasslands, and other land use types. However, a positive association was observed with edge density in this species (Table 5). *S. turtur* was negatively associated with urban areas and edge density. However, it showed a positive association with grasslands (Table 6).

Species richness was positively associated with urban areas and edge density. However, coniferous forests and land use richness showed a negative association with species richness (Table 7).

Table 2. GLM model results accounting for the presence and absence of species feral pigeon (*Columba livia forma domestica*) concerning different land use types, land use richness, and edge density in 2016. Abbreviations: SE—standard error. Significant variables are highlighted in bold.

	Estimate	SE	z-Value	*p*-Value
(Intercept)	**−1.136**	**0.393**	**−2.891**	**0.004**
Deciduous forest	**−0.042**	**0.008**	**−4.927**	**<0.001**
Coniferous forest	**−0.043**	**0.008**	**−5.708**	**<0.001**
Mixed forest	**−0.030**	**0.008**	**−3.971**	**<0.001**
Farmland	**−0.013**	**0.004**	**−3.398**	**0.001**
Grassland	**−0.024**	**0.006**	**−3.713**	**<0.001**
Urban	0.004	0.004	1.227	0.220
Other land use types	**−0.010**	**0.005**	**−1.847**	**0.065**
Land use richness	−0.051	0.063	−0.803	0.422
Edge density	**3.771**	**1.627**	**2.318**	**0.020**

Table 3. GLM model results accounting for the presence and absence of species stock dove (*Columba oenas*) concerning different land use types, land use richness, and edge density in 2016. Abbreviations: SE—standard error. Significant variables are highlighted in bold.

	Estimate	SE	z-Value	*p*-Value
(Intercept)	**−2.247**	**0.251**	**−8.962**	**<0.001**
Deciduous forest	**0.020**	**0.003**	**7.328**	**<0.001**
Mixed forest	**0.007**	**0.004**	**2.081**	**0.037**
Grassland	−0.007	0.005	−1.248	0.212
Farmland	**−0.007**	**0.003**	**−2.412**	**0.016**
Urban	**−0.013**	**0.006**	**−2.129**	**0.033**
Other	−0.002	0.006	−0.422	0.673
Land use richness	−0.005	0.073	−0.065	0.948
Edge density	−5.300	3.507	−1.511	0.131

Table 4. GLM model results accounting for the presence and absence of species wood pigeon (*Columba palumbus*) concerning different land use types, land use richness, and edge density in 2016. Abbreviations: SE—standard error. Significant variables are highlighted in bold.

	Estimate	SE	z-Value	*p*-Value
(Intercept)	0.245	0.291	0.842	0.4
Deciduous forest	0.002	0.003	0.745	0.456
Coniferous forest	**0.008**	**0.003**	**2.595**	**0.009**
Mixed forest	**0.007**	**0.003**	**2.081**	**0.037**
Farmland	−0.001	0.003	−0.354	0.723
Grassland	0.000	0.003	0.053	0.958
Urban	−0.004	0.003	−1.384	0.166
Other land use types	−0.002	0.004	−0.431	0.666
Land use richness	−0.005	0.034	−0.161	0.872
Edge density	1.600	1.324	1.209	0.227

Table 5. GLM model results accounting for the presence and absence of species Eurasian collared dove (*Streptopelia decaocto*) concerning different land use types, land use richness, and edge density in 2016. Abbreviations: SE—standard error. Significant variables are highlighted in bold.

	Estimate	SE	z-Value	*p*-Value
(Intercept)	0.127	0.345	0.368	0.713
Deciduous forest	**−0.038**	**0.005**	**−8.412**	**<0.001**
Coniferous forest	**−0.044**	**0.005**	**−9.631**	**<0.001**
Mixed forest	**−0.027**	**0.004**	**−6.185**	**<0.001**
Farmland	**−0.015**	**0.003**	**−4.849**	**<0.001**
Grassland	**−0.026**	**0.004**	**−6.010**	**<0.001**
Urban	0.003	0.003	1.005	0.315
Other land use types	**−0.019**	**0.004**	**−4.376**	**<0.001**
Land use richness	−0.005	0.048	−0.113	0.910
Edge density	**7.805**	**1.966**	**3.970**	**<0.001**

Table 6. GLM model results accounting for the presence and absence of species European turtle dove (*Streptopelia turtur*) concerning different land use types, land use richness, and edge density in 2016. Abbreviations: SE—standard error. Significant variables are highlighted in bold.

	Estimate	SE	z-Value	*p*-Value
(Intercept)	**−0.995**	**0.175**	**−5.688**	**<0.001**
Deciduous forest	0.001	0.002	0.272	0.785
Mixed forest	−0.001	0.003	−0.215	0.830
Farmland	−0.001	0.002	−0.506	0.613
Grassland	**0.005**	**0.003**	**1.880**	**0.060**
Urban	**−0.013**	**0.004**	**−3.234**	**<0.001**
Other	0.003	0.003	0.739	0.460
Land use richness	−0.031	0.053	−0.582	0.561
Edge density	**−8.190**	**2.489**	**−3.291**	**<0.001**

Table 7. GLM model results accounting for species richness of five *Columbidae* species concerning different land use types, land use richness, and edge density in 2016. The included species are feral pigeon (*Columba livia forma domestica*), stock dove (*Columba oenas*), wood pigeon (*Columba palumbus*), Eurasian collared dove (*Streptopelia decaocto*), and European turtle dove (*Streptopelia turtur*). Abbreviations: SE—standard error. Significant variables are highlighted in bold.

	Estimate	SE	z-Value	*p*-Value
(Intercept)	**0.17**	**0.055**	**3.198**	**0.001**
Deciduous forest	<0.001	0.001	0.149	0.881
Mixed forest	<0.001	0.001	0.011	0.991
Coniferous forest	**−0.001**	**0.001**	**−1.702**	**0.089**
Grassland	−0.001	0.001	−0.993	0.320
Urban	**0.002**	**0.001**	**3.131**	**0.002**
Other	<0.001	0.001	−0.224	0.822
Land use richness	**−0.041**	**0.014**	**−2.995**	**0.003**
Edge density	**1.232**	**0.382**	**3.225**	**0.001**

4. Discussion

Our results confirmed the hypothesis of high habitat overlap among all five *Columbidae* species in farmland areas. However, they mainly co-exist in three land use types: Farmlands, forests, and urban areas. Furthermore, we recorded an almost complete habitat overlap between *C. livia* and *S. decaocto*, as well as between *C. palumbus* and *S. turtur*. Regarding land use utilisation, *C. livia* and *S. decaocto* mainly utilised the farmlands and urban areas, and avoided all three types of forests (i.e., deciduous, coniferous, and mixed forests), grasslands, and other land use types. At the same time, forests were utilised mainly by *C. oenas* and *C. palumbus*. Specifically, *C. oenas* mainly utilised deciduous forests and avoided the farmlands and urban areas. *C. palumbus* utilised coniferous and mixed forests. Finally, *S. turtur* utilised mostly grasslands and avoided urban areas. Regarding species richness, it was higher in urban areas and areas with higher edge density. However, it was lower in coniferous forests and areas with higher land use richness.

Almost all of the complete habitat overlap between *C. livia* and *S. decaocto* was associated with their presence in areas with higher edge density, i.e., in urban areas. Therefore, habitat overlap between these two species is not surprising since both species are common in urban avian assemblages [21]. Additionally, high habitat overlap was recorded between *C. palumbus* and *S. turtur*, mainly in farmlands, deciduous, and coniferous forests. The overlap of these species in farmlands occurred due to the fact that *C. palumbus*, which used to be a forest specialist, started colonising other habitats, such as farmlands in the 21st century in the Czech Republic [41]. In addition, *S. turtur* is a highly specialised species that has specific foraging habitat [42], which depends on open farmlands and grasslands [23]. Furthermore, *C. palumbus* was positively associated with forest, specifically coniferous and mixed stands, probably due to the fact that it depends on the shrubs and trees as nesting habitats [43]. However, several studies in western and northern Europe have reported that *C. palumbus* colonised urban areas in the beginning of the 21st century [20–22]. Although our results did not show a positive association between *C. palumbus* and urban areas, the species was present in cities. The lack of positive association in our study could be due to the fact that the colonisation process is still in progress since it started later in the eastern parts of Europe [11], including the Czech Republic or due to the sample bias and lack of sampling points in urban areas.

Regarding *C. oenas*, it had the lowest mean habitat overlap with all of the species. Therefore, it was the least congruent with other species distributions. However, the high habitat overlap occurred with *C. palumbus* mainly in forests, which aligns with the aforementioned results since both species utilise this land use type. Moreover, *C. oenas* was primarily present in deciduous and mixed forests since it depends on old beech trees for nesting [41]. Consequently, we can say that *C. oenas* is a forest specialist, confirmed by previous studies from the Czech Republic that have listed it as a forest species [44,45]. Furthermore, *C. oenas* showed a negative relationship with urban areas, which is in accord with its aforementioned preference for old trees [41], which are not common in cities. Regarding habitat overlap, *C. oenas* overlapped with *S. turtur*, the second highest habitat overlap from all of the other species, which is not surprising since both species feed on farmlands. According to a new study, populations of farmland specialists, including *S. turtur*, have declined in Europe since the 1980s [46]. Therefore, exploring the possibility of using *S. turtur* as an umbrella species is useful for future conservation measures.

In general, landscape heterogeneity did not play an essential factor in the spatial distribution of the studied species. The results show that land use richness does not seem to impact the presence or absence of any of the studied species. However, edge density was an important predictor for three species. *C. livia* and *S. decaocto* are primarily present in urban areas where land use richness is low and edge density is high due to small fragmented patches [47]. Next, *S. turtur* is a farmland specialist, and thus requires open habitats, such as farmlands, for feeding. In addition, it is negatively associated with edge density.

The higher species richness present in urban areas and areas with higher edge density was expected since most of the studied species are associated with cities, except for *S. turtur*. On the contrary, species richness was lower in coniferous forests and in more heterogeneous areas, in terms of land use richness.

Interestingly, no sampling point had all of the five species present, and only nine sampling points had four species present. From these patterns, we can speculate that an interspecific competition exists between these five species of *Columbidae*. Furthermore, our predictions that closely related species, pigeons, will have lower habitat overlap than distantly related species, pigeons and doves, were confirmed with several cases. Habitat overlap was the highest between *C. livia* and *S. decaocto*; *C. palumbus* and *S. turtur*; and finally, between *C. palumbus* and *S. decaocto*. However, additional detailed studies are necessary to further confirm this hypothesis.

5. Conclusions

In conclusion, our results showed that the *Columbidae* species mainly co-exist in three land use types: Urban areas, forests, and farmlands. With the highest species richness in urban areas and areas with high edge density, this indicates that species have high tolerance to anthropogenic disturbances in cities. *C. livia* and *S. decaocto* had high habitat overlap in urban areas; *C. oenas* and *C. palumbus* had high habitat overlap in forests; and *C. palumbus* and *S. turtur* had high habitat overlap in farmlands. Furthermore, our research assumes that *S. turtur* can serve as an umbrella species for lowering the hunting pressure on other farmland and grassland species. Finally, our results provide a comprehensive insight into these common species habitat affinities and utilisation. Further research is necessary to understand the reasons behind drivers of their co-existence in these habitats.

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