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Distribution and protection of avian specialization in Europe

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Abstract

Aim: We assessed the spatial distribution of four different types of avian specialization throughout Europe, identifying landscape features associated with specialization and quantifying where the Natura 2000 network intersects with areas of high avian specialization.

Location: Europe.

Time period: Present day.

Taxa studied: European breeding birds.

Methods: We used the European Atlas of breeding birds and four avian specialization measures (diet, foraging behaviour, foraging substrate and habitat). We calculated specialization richness and identified geographical hotspots for each of these ecological traits. We tested whether elevational gradient, landscape heterogeneity or dominant land use predicted each type of specialization richness. We determined which types of European protected areas are most associated with higher specialization richness.

Results: Diet and foraging substrate specialists increased with elevation, whereas richness of foraging behavioural specialists decreased. There was a greater richness of dietary and habitat specialists in forests than in other environments. The Natura 2000 areas declared under Bird and both directives (Birds and Habitats) intersected with a high dietary, foraging substrate and habitat specialist richness. The richness of foraging behaviour specialists was high in Birds directive areas. Single and multiple hotspots of specialization were greater in protected than non-protected areas. However, almost 30% of specialization hotspots did not intersect with protected areas.

Main conclusions: Our findings suggest that higher levels of avian specialization in Europe are positively associated with elevation and forested land cover. Importantly, we found that the Natura 2000 network supports all types of avian ecological specialization, albeit mainly in areas declared under both directives.

KEYWORDS

avian distribution, avian specialization, birds, conservation, Natura 2000 network, protected areas

1 | INTRODUCTION

Anthropic activities, such as transforming natural habitats (i.e., crops, pasture and infrastructure), are the main drivers of current species declines (IUCN, 2015; Maxwell et al., 2016). These changes are accelerating rapidly (Steffen et al., 2015), harming natural environments (Newbold et al., 2015; Venter et al., 2016) and driving many species to extinction (IUCN, 2015). Another major threat affecting global diversity is climate change, driving species to extinction and causing niche shifts (Román-Palacios & Wiens, 2020). Hence, there is an urgent need to improve biodiversity conservation efforts (Butchart et al., 2015). The protected area network is a keystone of global conservation efforts (Bastian, 2013; Watson et al., 2014), safeguarding biodiversity by reducing habitat loss and overexploitation, among other threats (Margules & Pressey, 2000). Correct placement of protected areas is crucial in ensuring maximal protection of biodiversity from adverse effects of anthropogenic pressures (Akasaka et al., 2017; Fuller et al., 2010; Hanson et al., 2020).

Taxonomic diversity (e.g., species richness) is often used to identify candidate protected areas (Bonn & Gaston, 2005). The ultimate goal is to maximize the overall number of species represented among protected areas. Species richness is intuitive and relatively cost effective to quantify (Cadotte et al., 2010). Recently, several studies have argued that the selection of protected areas based on species richness should be reviewed (e.g., Albuquerque et al., 2015; Astudillo-Scalia & Albuquerque, 2020), and further methods were proposed to select protected areas more efficiently (e.g., using complementarity-based algorithms; Albuquerque & Beier, 2015; Astudillo-Scalia & Albuquerque, 2020; Ware et al., 2018). Additionally, species richness fails to capture essential aspects of biodiversity that could be considered in delineating protected areas (Astudillo-Scalia & de Albuquerque, 2019). In Europe, the Natura 2000 network (the largest regional network of protected areas in the world) aims to preserve special habitats and priority species (targeted) under two primary directives. The first is the Habitats directive (Directive 92/43/EEC, 1992), which has two components: (1) Sites of Community Importance; and (2) Special Areas of Conservation. Both components of this directive are used to conserve biodiversity (i.e., relevant species and habitat) across Europe. The second directive is the Birds directive (Directive, 2009/147/EC, 2009), under which Special Protected Areas (SPAs) are declared, focused on the conservation of wild birds in EU countries. These directives represent the basis for protected area planning in Europe.

Recent studies have highlighted how the Natura 2000 network also protects non-target common species in addition to specifically targeted species (Kukkala et al., 2016; Lisón et al., 2015). This is important, because many common species are declining at a rapid rate (Inger et al., 2014), and such declines are likely to impact macroecological patterns and ecosystem functioning negatively (Baker et al., 2019; Gaston, 2010; Gaston & Fuller, 2008). Indeed, the performance of protected area planning strategies has been evaluated through the assessment of different avian diversity facets of species communities, such as functional and phylogenetic diversity (Benedetti et al., 2020; Jetz et al., 2014). One crucial aspect of species communities that has received relatively less attention in evaluating protected area systems is ecological specialization (Morelli et al., 2019). However, this aspect deserves more attention because specialist species possess narrower niche breadths, hence lower capacity to respond to anthropogenic disturbance (Devictor et al., 2008). Specialist species have a higher extinction risk than non-specialists (Balisi et al., 2018; Colles et al., 2009; Devictor, Julliard, & Jiguet, 2008), and many European specialist bird species are in rapid decline (Bowler et al., 2019; Stephens et al., 2016), highlighting the need to consider ecological specialization in conservation planning (Morelli et al., 2019, 2021).

The first classifications of specialization were based on a binomial categorization, such as habitat "specialist" or "generalist" (Gregory et al., 2005). More recently, several studies have positioned species along a gradient of specialization (e.g. diet type, habitat breadth; Devictor, Julliard, & Jiguet, 2008; Luck et al., 2013; Moreira et al., 2001), although many studies exploring patterns of avian specialization gradients focus on only one or two niche dimensions (Barnagaud et al., 2017, 2019; Belmaker et al., 2012; Mimet et al., 2019; Morelli et al., 2021; Rivas-Salvador et al., 2019). Devictor et al. (2010) characterized specialization as a syndrome-like modification of several traits to allow for effective exploitation of specific resources. Thus, specialization can vary across multiple niche dimensions (e.g., a species could be specialized in selection of breeding habitats while being generalist in a dietary trait). Thus, measures of ecological specialization are best thought of as multidimensional (Devictor, Julliard, & Jiguet, 2008; Luck et al., 2013), using data on multiple traits of species, such as behaviour, habitat or diet (Devictor et al., 2010). This multidimensional approach allows for the identification of species that might be vulnerable to a range of anthropogenic threats and require special conservation measures (Hatfield et al., 2018; Henle et al., 2004).

Considering the rapidity of declines in biodiversity, knowledge of how change in land use influences ecological organization is essential for conservation planning (Sirami et al., 2017). Many studies have shown that species distributions are influenced by landscape variables (Melillo et al., 1993; Newbold et al., 2018). For example, avian species richness is associated with latitude (Hillebrand, 2004; Stevens, 1989), elevation (Lomolino, 2001; Rahbek, 1995; Stevens, 1992) and land-use heterogeneity (Morelli et al., 2013; Stein et al., 2014). Moreover, habitat fragmentation and landscape heterogeneity drive changes in assemblage composition (Fuller et al., 1997; Morelli, 2012; Schindler et al., 2008; Suarez-Rubio & Thomlinson, 2009) because high habitat diversity is associated with an increase in niche availability for species (Kisel et al., 2011). Variation in geographical and landscape features can strongly influence species distributions and cause turnover in communities (Barnagaud et al., 2017; Hillebrand et al., 2018), potentially facilitating the insertion of generalist species and the loss of specialist and/or endemic species (Devictor, Julliard, Clavel, et al., 2008), leading to global biotic homogenization (Davey et al., 2012; McKinney & Lockwood, 1999). However, the underlying geographical drivers for ecological specialization and the extent to which existing European protected areas support specialist species remain unclear.

At a continental scale, studies have revealed some spatial patterns in avian specialization. For example, there is a positive relationship in European birds between elevation and the community specialization index (CSI) (Rivas-Salvador et al., 2019). In North America, land use influences bird habitat and climate specialization, with specialization being lower in human-dominated areas (Mimet et al., 2019). In Europe, where changes in land use have unfolded somewhat differently than in North America, studies are fewer and limited to dietary specialization. These studies show a pattern of loss of specialist species as the human footprint increases (Barnagaud et al., 2017, 2019). To maximize the value of protected areas for biodiversity conservation, we must understand the relationship between multiple types of specialization and landscape characteristics, highlighting the areas with a high number of specialist species. Also, more in-depth knowledge of the spatial pattern of distribution of specialization in Europe will help to inform the new European Biodiversity Strategy for 2030, which aims to increase the EU-wide network of protected areas based on the existing Natura 2000 areas and focus on strict protection of areas with high biodiversity value (EC, 2020).

Here, our main objective was to explore the spatial distribution of different types of avian ecological specialization and the extent to which specialist species are represented in protected areas in Europe. Initially, we mapped the spatial distribution of four dimensions of avian specialization and explored whether some landscape characteristics (e.g., dominant land use, landscape heterogeneity and elevation) influence their distribution. Then we measured the extent to which different types of Natura 2000 areas intersect with avian specialization, highlighting regions potentially important for expanding protected area designations.

2 | METHODS

2.1 | Mapping European bird communities

We used the 50 km × 50 km European Ornithological Atlas (EOA) grid cells (hereafter referred to as "cells"), a version of the CGRS grid edited in 2006 (Hagemeijer & Blair, 1997), to obtain the European bird species communities by mapping the Atlas of European Breeding Birds EBBA1 from European Bird Census Council (EBCC) (Hagemeijer & Blair, 1997) using ArcGIS v.10.1 (ESRI, 2012). The EBBA1 data cover 499 avian breeding species, and this is a flagship programme of the EBCC (conceived by merging the European Ornithological Atlas Committee and the EBCC). The EBBA1 was published in 1997, synthesizing 25 years of avian survey data and combining the efforts of thousands of volunteer field ornithologists, data analysts and authors from 40 European countries. The quality of the EBBA1 will inevitably vary spatially (see details described by Hagemeijer & Blair, 1997), although the majority of the 50 km × 50 km grid cells used in the present study had high-quality coverage by bird surveys (Hagemeijer & Blair, 1997). To reduce potential bias from variation in coverage, we removed from the analysis those EBBA1 squares with fewer than six bird species, considering such squares to be surveyed incompletely. For further details on the quality and reliability of the data on breeding avian species distribution in Europe, see Huntley et al. (2007).

2.2 | Mapping elevational gradient, land-use composition and protected areas network

To map the European elevational gradient, we used data from the Shuttle Radar Topography Mission (SRTM) v.4.1 (Jarvis et al., 2008) in decimal degrees and datum WGS84. The data on elevation were derived using the United States Geological Survey/NASA (USGS/NASA) SRTM data, transformed in a continuous topography surface through interpolation methods (Reuter et al., 2007). We calculated the mean elevation (in metres) in each 50 km × 50 km cell, using "zonal statistics" from Spatial Analyst tools in ArcGIS v.10.1 (ESRI, 2012).

To determine dominant land use, we considered the percentage of different land uses within each 50 km × 50 km cell. Types of land use were based on the CORINE land cover (CLC) vector data derived from 25-m resolution satellite data 2018. CLC is a national georeferenced land cover database available for the EU, based on digital satellite images (Bossard et al., 2000). The CLC system includes 44 land cover classes (EEA, 1994). In the present study, land-use categories were reclassified to obtain seven land-use types: agriculture, forest, grassland, mixed, semi-natural, urban and water. The percentage of each type of land use was obtained through the "intersect operator" function in ArcGIS v.10.1 (ESRI, 2012). Reflecting dominant land use, each cell was classified into a land-use category when the main land use was > 50% (e.g. Morelli et al., 2013), except for the category urban, which was classified as dominant where it occupied ≥ 30% and all other categories individually comprised ≤ 50% of the land area. The cells with mixed composition, where none of the land-use types occupied ≥ 50% of the area, were classified as mixed environments.

Bird species richness is known to be correlated with patterns of landscape heterogeneity (Morelli et al., 2013); therefore, we calculated two landscape metrics (Shannon–Weaver diversity index and land-use richness) often used in ecological studies (Morelli et al., 2013). We assessed the Shannon–Weaver diversity index (a measure of compositional landscape heterogeneity and habitat diversity; Kisel et al., 2011) with the formula $H = \sum \mathrm{pi} \ln(\mathrm{pi})$, where pi values represent the percentages of different land-use types within each 50 km × 50 km cell. Land-use richness was measured as the number of different types of land uses within each 50 km × 50 km cell.

For mapping the Natura 2000 protected areas network, we used the shapefile available from the Natura 2000 website (European Environment Agency, 2019). We mapped the Natura 2000 areas declared under the Birds directive, the Habitats directive and "both directives" (Supporting Information Table S1; Figure S1). We calculated the intersection of each 50 km × 50 km EOA cell with each type of Natura 2000 protected area, using the "intersect operator" from Spatial Analyst tools in ArcGIS v.10.1 (ESRI, 2012). Each cell was classified as: (1) non-protected; (2) area protected under the Habitats directive; (3) area protected under the Birds directive; or (4) area protected under both directives, using a threshold of > 60% of the protected area cover.

2.3 | Mapping avian specialization of the species community

A bird community was considered as the total list of bird species present in each 50 km × 50 km cell. Thus, species richness was estimated as the total number of bird species in each cell (Magurran, 2004). This study focused on avian specialization indices based on a trait approach from Morelli et al., 2019. We considered four different categories of avian traits (diet, foraging behaviour, foraging substrate and habitat) comprising 42 underlying variables (Supporting Information Table S2), indicating the ecological niche exploited by each species (Pearman et al., 2014; Storchová & Hořák, 2018). Each specialization index was calculated for all species in the dataset using the Gini index of inequity (Colwell, 2011; Gini, 1921). The Gini coefficient measures statistical dispersion and can take on values between zero and one, indicating low to high specialization. Through this procedure, Morelli et al. (2019) created, for 365 avian species, five specialization indices: dietary specialism, foraging behaviour specialism, foraging substrate specialism, general habitat specialism and nesting site specialism. Given that very few avian species were classified as nesting site specialists, we excluded this category of specialization from further analyses. The complete list of specialization indices is provided in the Supporting Information (Table S3). We estimated "specialist richness" for each category of specialization in each cell by counting the number of species with an index value of one. We chose only the species with the most specialized species, hence those that need more conservation attention. With this approach, *c*. 30% of bird species are classified as specialists (see more details in Supporting Information Table S3).

We mapped the spatial distribution of bird species richness and each type of specialist richness (Figure 1) using the Jenks optimization method. This data-clustering method guarantees an optimized visualization by clustering the arrangement of values into different classes using breakpoints based on the values provided for clustering (Jenks, 1967). This method is suitable for visualizing and identifying spatial patterns (Menéndez-Guerrero & Graham, 2013). We defined the number of classes as six after initial exploration of other numbers of classes showed qualitatively similar results for each category of specialization. Values represented six classes in each variable going from lower to upper class to ensure an optimal visualization of values with well-representable colours. Then, we defined like hotspots of each avian specialization category as the upper or top class of each clustering optimization, corresponding to the greatest values of richness for each type of specialization. Finally, considering all specialization categories, we estimated the number of hotspots in each 50 km × 50 km cell and classified the cell as single (single-HS) when

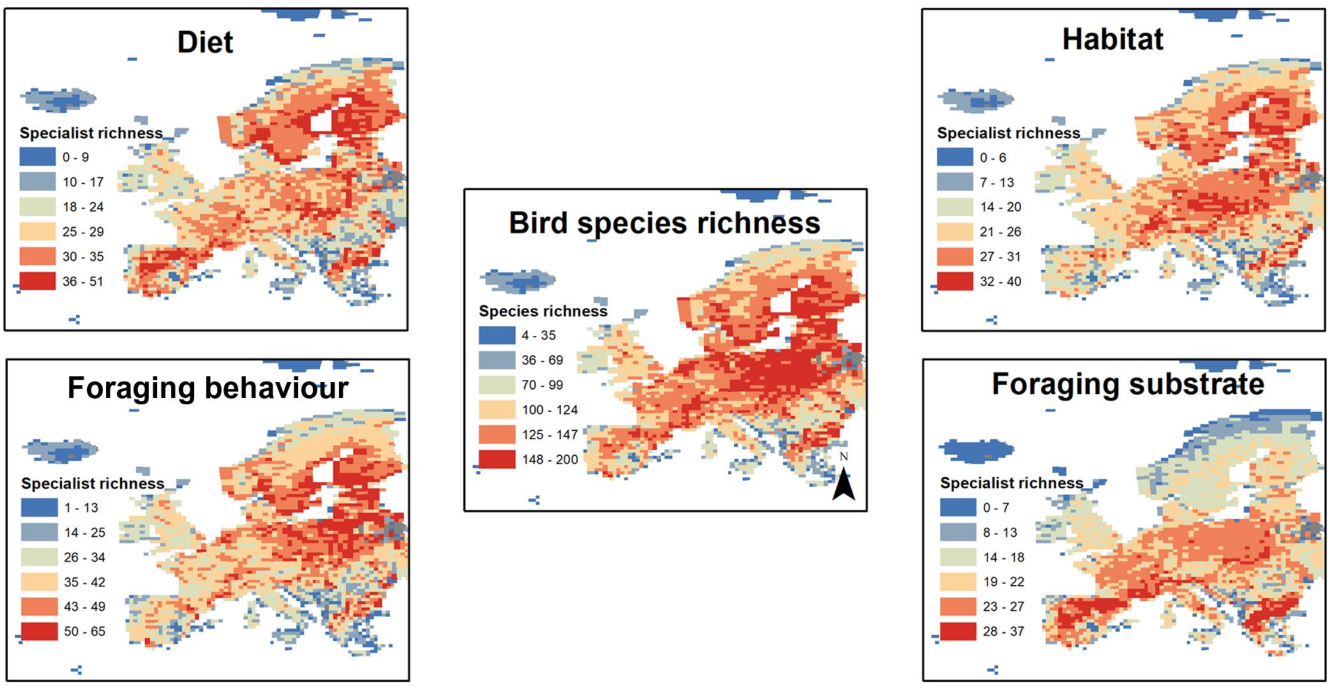

FIGURE 1 European distribution of breeding bird species richness and four types of specialist richness. The values are presented in a colour gradient from lower (blue) to moderate (light green and yellow) to higher (red). The spatial unit used for mapping the values is a grid of 50 km × 50 km cells covering Europe. For the visualization of data, we used the natural breaks (Jenks) classification method

the number of hotspots was one, multiple (multiple-HS) when the number of hotspots was higher than one, and non-hotspot (non-HS) when there were no hotspots of any specialization.

2.4 | Statistical analysis

We applied two different spatially explicit correlation tests to assess: (1) potential spatial autocorrelation in each response variable; and (2) spatial association among avian specialization richness. Specifically, to test spatial autocorrelation, we used a Mantel test (Legendre & Fortin, 2010; Mantel, 1967) to examine the correlation between pairwise geographical distances of centroids of 50 km × 50 km cells and the pairwise avian specialization richness distances (Euclidean) across all 50 km × 50 km cells (Supporting Information Table S4). To test spatial associations among all avian specialization richness types, we contrasted distance matrices with differences among each avian specialization richness across all 50 km × 50 km cells (Supporting Information Table S5). Mantel test significance was obtained applying Monte Carlo permutations with 999 randomizations (Oksanen et al., 2016), running the package "ade4" for R (Dray & Dufour, 2007).

Linear regression (GLS) models were used to assess individual relationships between each type of specialization richness and landscape characteristics. GLS permits consideration of the spatial autocorrelation detected in all categories of specialization. We used GLS models with a Gaussian correlation structure with the function "corGaus(form = ~lat + long)", including the latitude and longitude of each cell (Dormann et al., 2007). Dietary specialist richness, foraging behaviour specialist richness, foraging substrate specialist richness and habitat specialist richness were modelled separately as response variables. All response variables followed an approximately normal distribution without further transformation (Supporting Information Figure S2). As predictors, we used bird species richness and the following spatial variables: dominant land use (agriculture, forest, grassland, mixed, semi-natural, urban and water), mean elevation and landscape metrics (specifically, land-use diversity and land-use richness). The number of specialist species and overall bird species richness showed a strong association, which is expected because the former is a subset of the latter (Supporting Information Figure S3). Thus, to control for a potential bias effect, we included species richness as a covariate in each specialization richness model, rather than in a regression of their residuals as suggested by Freckleton (2002). Variance inflation factors (VIFs) were used to explore potential multicollinearity among predictors (e.g., species richness, dominant environment, landscape heterogeneity and elevation) using the "fmsb" package (Nakazawa, 2017). The VIF values of all predictors were less than five, hence all predictors were incorporated in the modelling procedure. Models were fitted by maximum likelihood, using the "nlme" package in R (Pinheiro et al., 2019). Akaike's information criterion (AIC) was used to identify the model that "best" explained variation in the data, characterized by the lower AIC (Burnham & Anderson, 2002). Finally, we used the Wald method from the package "mass" (Venables & Ripley, 2002) to estimate confidence intervals for significant variables.

We tested whether each type of specialization richness differed significantly among types of protected areas (Birds directive, Habitats directive and both directives) and in non-protected areas. To do this, we applied a Kruskal–Wallis *H* test (significance $\alpha = .05$ probability) by using the "kruskal.test" function in R. Subsequently, we ran post hoc pairwise comparisons with Bonferroni adjustment using the function "posthoc.kruskal.dunn.test" with the "PMCMR" package in R (Pohlert, 2014).

Additionally, differences in hotspots of specialization intersecting each type of Natura 2000 protected areas and non-protected areas were compared with a chi-square test. Subsequently, a series of post hoc pairwise comparisons were conducted to identify differences between specific combinations of hotspots (non-hotspots, single hotspots and multiple hotspots) and protected area types (Birds directive, Habitats directive and both directives). We ran post hoc pairwise comparisons with the false discovery rate adjustment using the function "chisq.multcomp" with the "RVAideMemoire" package in R (Hervé, 2020).

All statistical tests were performed in R v.3.5.3 (R Development Core Team, 2019).

3 | RESULTS

After the intersection of all layers (EBCC, USGS/NASA SRTM data, CLC and Natura 2000 protected areas network), we obtained a total of 2,511 grid cells with complete information on avian species, elevation, land-use composition and protected and non-protected areas. The Natura 2000 intersects a total of 1,302 (52%) grid cells, of which 272 were declared under the Birds directive, 342 under the Habitats directive and 688 under both directives. The remaining grid cells (1,209) are non-protected.

In the total 2,511 grid cells covering Europe were recorded 337 breeding bird species. From the total number of avian species, 102 species were classified as dietary specialists (30.3%), 133 species as foraging specialists (39.5%), 62 species as foraging substrate specialists (18.4%) and 88 species as habitat specialists (26.11%). Subsequently, we assessed the spatial distribution of species richness and the number of specialist birds throughout Europe (Figure 1). All categories of specialists were not randomly distributed and were spatially clumped (Supporting Information Table S4). Specialist richness for all categories was spatially associated with each other (Supporting Information Table S5). The highest spatial association was found between foraging behaviour and habitat specialization, followed by the association between diet and foraging substrate specialization (Supporting Information Table S5).

The distribution of avian specialization hotspots was spatially different in Europe, depending on the specialization type (Figure 1). The most widespread hotspots were those for dietary specialization, reaching ≤ 51 different bird specialist species, and were mainly located in the Fennoscandian Peninsula and the Iberian Peninsula (Figure 1). In foraging substrate hotspots, we found ≤ 37 diverse specialist species, and these were concentrated mainly in Southern

Europe (Figure 1). Foraging behaviour hotspots were located mainly in Eastern Europe and the Fennoscandian Peninsula, comprising ≤ 65 different specialist species (Figure 1). Lastly, habitat hotspots occurred mainly in central and Eastern Europe, comprising ≤ 40 different specialist species (Figure 1).

The distribution of specialist species was correlated with different landscape variables depending on the specialization category. We found a greater number of dietary and foraging substrate specialists at higher elevations, whereas mean elevation was negatively associated with the richness of foraging behaviour specialists (Table 1; Supporting Information Figure S4). In forested cells, we found a higher number of specialists in diet and habitat (Table 1; Supporting Information Figure S5). Moreover, we found a relatively small number of foraging substrate specialists in forested, semi-natural and water cells (Table 1; Supporting Information Figure S5). Additionally, no specialist types were significantly correlated with the landscape heterogeneity metrics (Table 1).

The Natura 2000 areas declared under Birds and both directives (Birds and Habitats) intersected with a greater richness of dietary, foraging substrate and habitat specialists (Figure 2; Supporting Information Table S6; Figure S6). The richness of foraging behaviour specialists was greater under Birds directive protected areas (Figure 2; Supporting Information Table S6; Figure S6). The richness of all types of specialization was lower in non-protected areas (Figure 2; Supporting Information Table S6; Figure S6). The number of single and multiple hotspots of specialization was also higher in protected than non-protected areas (Figure 3; Supporting Information Table S7; Figure S7). Focusing on specialization hotspots, Figure 3 shows a greater percentage of single and multiple hotspots in protected areas declared under both directives than in those cells under Birds or Habitats directives (Figure 3; Supporting Information Table S7; Figure S7). Non-protected areas cells intersect almost 30% of total specialization hotspots and the greater percentage of non-hotspots cells (Figure 3; Supporting Information Table S7; Figure S7).

4 | DISCUSSION

4.1 | Spatial distribution of avian specialization

Previous work has focused on drivers shaping the spatial distribution of dietary and habitat specialization at a large spatial scale (Belmaker et al., 2012; Devictor, Julliard, & Jiguet, 2008; Mimet et al., 2019; Rivas-Salvador et al., 2019). However, a deeper understanding of additional life-history characteristics constricting the survival of specialist species is essential (Carscadden et al., 2020). The main novelty of our study is that we have mapped the spatial distribution of four different types of avian specialization throughout Europe, pinpointing the landscape features associated with specialization and quantifying how the Natura 2000 network intersects areas of high avian

TABLE 1 Results of the linear regression (GLS) model performed in this study, accounting for variations in each category of specialization concerning the following predictors: bird species richness, mean elevation, land-use diversity, land-use richness and the different types of dominant land use (agriculture, forest, grassland, mixed, semi-natural, urban and water)

Predictor variable	Estimate	*SE*	*t*/*z*	*p*-value
Response variable: Dietary specialization				
Intercept	−1.730	.332	−5.210	<.01
Bird species richness	.233	.002	120.730	<.001
Mean elevation	.001	.000	3.330	<.01
Forest	.580	.173	3.360	<.01
Response variable: Foraging behaviour specialization				
Intercept	−1.270	.263	−4.835	<.001
Bird species richness	.327	.002	168.64	<.001
Mean elevation	−0.003	.000	−14.880	<.001
Response variable: Foraging substrate specialization				
Intercept	−0.887	.414	−2.142	<.01
Bird species richness	.159	.002	80.600	<.001
Mean elevation	.001	.000	6.631	<.001
Forest	−0.493	.177	−2.793	<.01
Semi-natural	−0.573	.214	−2.672	<.01
Water	−0.551	.201	−2.736	<.01
Response variable: Habitat specialization				
Intercept	−2.540	.300	−8.750	<.001
Bird species richness	.211	.002	109.800	<.001
Forest	.417	.171	2.440	<.05

Note: Outputs of the best models are shown in the table. The full models are shown in the Supporting Information (Table S8). Akaike's information criterion values for each model performed in this study are shown in the Supporting Information (Table S9).

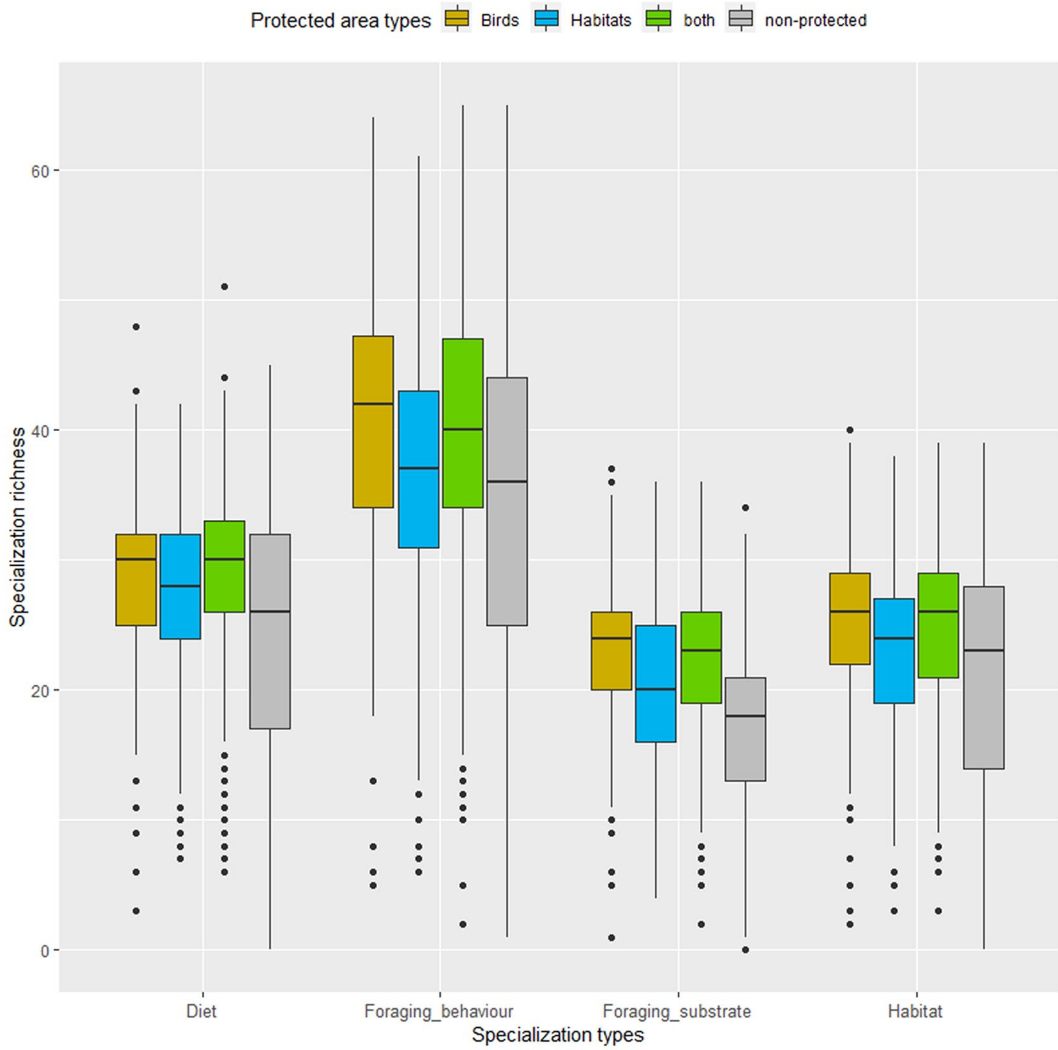

FIGURE 2 Comparison of each type of Natura 2000 protected area (Habitats directive, Birds directive and both directives) and non-protected areas intersecting each type of specialization richness (diet, foraging behaviour, foraging substrate and habitat). The *y* axis represents the estimated variable, the number of specialist species. Box plots show the median (the bar in the middle of rectangles), upper and lower quartiles (lenght of rectangles), maximum and minimum values (whiskers), and extreme values (black dots). Significant differences are shown in the Supporting Information (Table S6)

specialization. Additionally, we identified areas where many specialization types are spatially congruent, highlighting potential vulnerability to anthropogenic environmental change.

Our results demonstrated a positive correlation between species richness and avian specialization across four different specialization categories (diet, foraging behaviour, foraging substrate and habitat) in European breeding bird communities. These findings agree with previous studies at global and continental scales focused on different taxa and specialization types (Belmaker et al., 2012; Granot & Belmaker, 2020). The first implication of these results is that conservation planning focusing on avian species richness could also protect a high degree of species specialization in Europe, highlighting the potential value of species richness as a cost-effective conservation tool (Fleishman et al., 2006). However, our results have shown that the correlation between species richness and the number of specialist birds is not strong enough to guarantee a perfect match. Figure 1 highlights areas where the congruence is high, but also areas where a mismatch is clear. The congruence between species richness and specialization richness was particularly high in Fennoscandia and the Balkan Peninsula for dietary specialists, in Fennoscandia and eastern Europe for foraging behaviour specialists and in Fennoscandia for habitat specialists. In contrast, mismatch between species richness and specialization richness was particularly high in the Iberian Peninsula and eastern Europe for dietary specialists, in eastern Europe for foraging behaviour and habitat specialists and in Fennoscandia and eastern Europe for foraging substrate specialists. Likewise, the spatial congruence between specialization types highlights areas characterized by avian communities with high overall specialization richness. In areas characterized by a high congruence between species richness and specialization richness, conservation strategies focused mainly on species richness could be more effective in also protecting ecological specialists. However,

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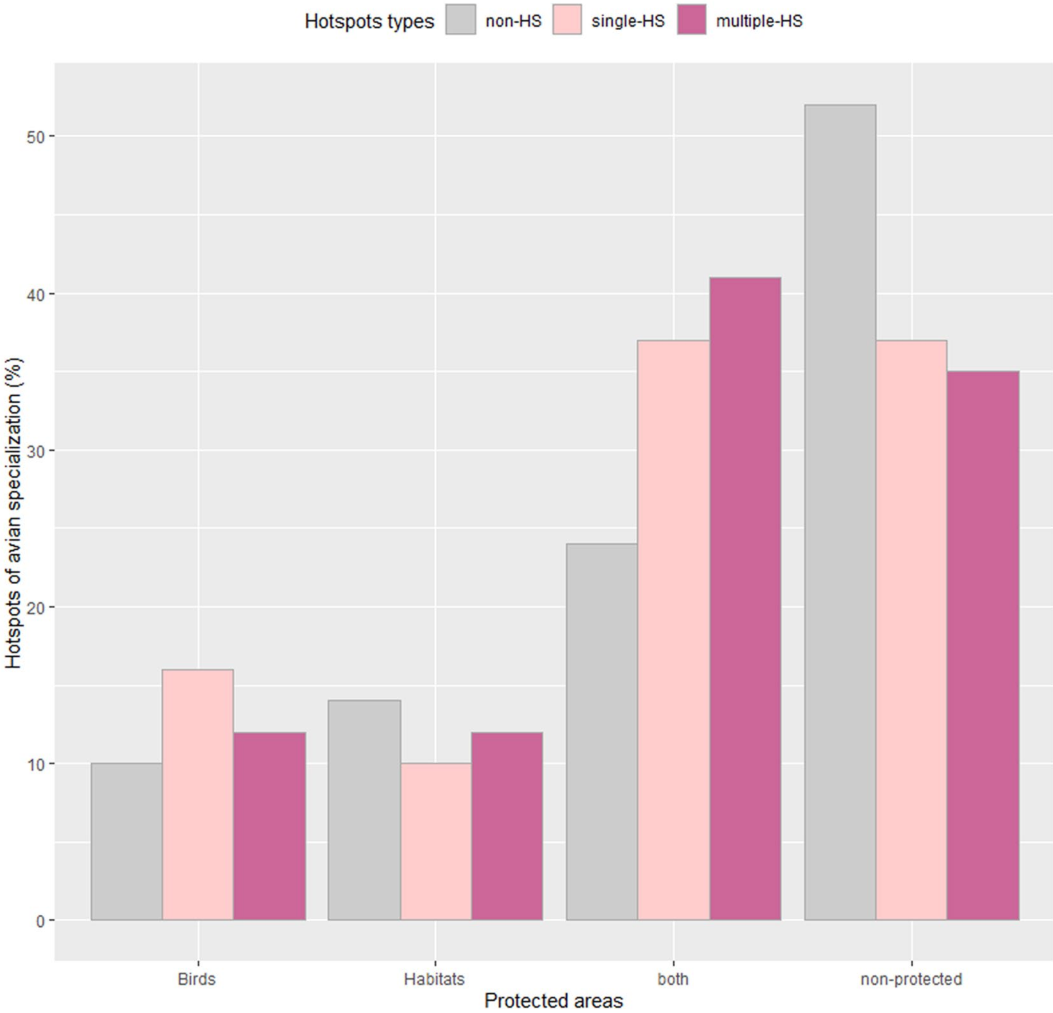

FIGURE 3 Bar chart showing the distribution of specialization hotspots (single-HS and multiple-HS) and non-HS intersecting each type of Natura 2000 protected area (Habitats directive, Birds directive and both directives) and non-protected areas. To estimate single-HS and multiple-HS, all types of specialization hotspots (diet, foraging behaviour, foraging substrate and habitat) were grouped. Each bar of the same colour indicates the total number of cells (as a percentage) of each type of specialization hotspot (single-HS and multiple-HS) and non-HS, and bars of the same colour sum to 100%. Significative differences of comparisons between hotspot types in each protected area type are shown in the Supporting Information (Table S7)

often species richness cannot capture significant facets of biodiversity to delineate protected areas efficiently (Astudillo-Scalia & de Albuquerque, 2019). Accordingly, several studies claimed a review of the criteria based only on the species richness (e.g., Albuquerque et al., 2015; Astudillo-Scalia & Albuquerque, 2020). Thus, our findings are congruent with the studies mentioned and make evident a need to include specialization in conservation planning in regional and European strategies to protect specialized species further.

4.2 | Association between avian specialization and landscape characteristics

Elevation is a driver influencing changes in avian communities (McCain, 2009). We found that higher elevations were significantly associated with species more specialist in diet and foraging substrate. These results reflect those observed in another European study that used a different specialization index, the habitat CSI, which showed increasing specialization towards higher elevations (Rivas-Salvador et al., 2019). In our study, however, the number of habitat specialists was not statistically correlated with elevation. Such differences could stem from the different types of indices used in both studies. Rivas-Salvador et al. (2019) used the CSI, which characterizes avian communities using mean and *SD* values, whereas our index is based on the total number of habitat specialists in each community. Therefore, a direct comparison is inappropriate. A widely recognized pattern in macroecology is that the number of avian species decreases at higher elevations (Stevens, 1992). Spatial hypotheses suggest that such decline could be related to spatial constraints facing montane species (Pan et al., 2016; Sanders & Rahbek, 2012). However, several studies have suggested different and complex impacts of environmental drivers on species distribution across an elevational gradient (McCain, 2009; Rahbek, 2005). The climate (i.e., the variability of climate throughout Europe) is one potential mechanism explaining our results and the distribution of specialization throughout Europe and is also broadly supported by other studies (e.g., McCain, 2009). For example, the temperature is a major driver that decreases with elevation, influencing the physiological tolerance of birds (Currie et al., 2004; Pan et al., 2016) and affecting the vegetation and availability of food resources (Kim et al., 2018). Owing to the sharp elevational habitat gradients, unique climate regions in Europe (e.g., mountain areas) could be associated with hotspots of avian endemism (Orme et al., 2005) and specialization (Jankowski et al., 2013).

Investigating the relationship between land use and specialization, we found more dietary and habitat specialist species in forested areas. A previous study demonstrated the strong relationship between avian species distribution and vegetation structure (Gil-Tena et al., 2007). Additionally, other studies showed that forested areas hold more heterogeneous and specialized bird communities (Benedetti et al., 2021; Kirk & Hobson, 2001). This is because forests provide a high number and diversity of tree-related microhabitats (Asbeck et al., 2019), food availability for some insectivorous birds (Redolfi De Zan et al., 2017), and offer several environmental resources for specialist birds to meet their specific needs of food and habitat requirements (Kühnert et al., 2019; Schaaf et al., 2020).

Overall, our work highlights the importance of high elevations and forested areas in future conservation planning for specialist species. A higher number of dietary specialists in the water land-use class might have been expected. However, we hypothesize that given the spatial scale of the analysis, cells dominated by water will often also contain many other land uses. For example, in cells dominated by water we found, on average, the following land uses: urban (1.3%), agriculture (6.4%), grassland (2.7%), shrub (8%) and forest (5.2%). Thus, generalist species associated with different land uses might reduce the overall level of specialization of those communities. In contrast, we found different responses to landscape variables for foraging behaviour specialists and foraging substrate specialists, with fewer foraging behaviour specialists at higher elevations and fewer foraging substrate specialists in forested and water areas. Considering that landscape heterogeneity is positively correlated with bird species richness (Morelli et al., 2013), we expected similar responses for specialization. However, all categories of specialization considered in the present study were not strongly correlated with landscape heterogeneity measures. Possible explanations for this result include: (1) the abundance of certain species or particular avian guilds is related more to the dominant land use than to the landscape configuration (Carrara et al., 2015; Uuemaa et al., 2013); (2) particular avian guilds have different associations with specific landscape metrics (Borges et al., 2017; Mimet et al., 2014); (3) higher habitat heterogeneity could be related to the occurrence of more species adapted to living in multiple environments (i.e., generalists); and (4) given that spatial scale affects the strength of the association between landscape metrics and terrestrial birds (Morelli, 2013; Schindler et al., 2013), the spatial resolution used in this study, even if suitable for detecting spatial patterns at a biogeographical scale, could be too coarse to explore the association between the landscape heterogeneity and the number of avian specialist species in the communities.

4.3 | Protected areas and conservation of avian specialization

Most threatened European bird species are declining (BirdLife International, 2012a, 2012b), and the European directives for Habitats (Directive 92/43/EEC, 1992) and Birds (Directive, 2009/147/EC, 2009) provide conservation measures to maintain the natural and semi-natural habitats supporting bird populations. There is some evidence of an association between the pattern of bird species richness and the geographical distribution of SPAs across EU countries (Albuquerque et al., 2013). Nevertheless, clearer targets for the Natura 2000 network are necessary, including the identification of major threats and more effective management of protected areas. Considering the current global decline of specialist species from several taxa, such as plants (Rooney et al., 2004), insects (Warren et al., 2001), fishes (Munday, 2004), birds (Julliard et al., 2004) and mammals (Fisher et al., 2003), it is essential to consider the spatial associations between protected areas and ecological specialization. We found that the Natura 2000 network intersected areas with a greater avian specialization than non-protected areas. Considering that almost 50% of the protected territory under Natura 2000 is forested (Winkel et al., 2015), these results are congruent with the strong association between specialization and forest areas that we found in the present study. Among protected areas, those based on Birds and both directives have more dietary, foraging substrate, foraging behaviour and habitat specialist species than protected areas based on the Habitats (Directive 92/43/EEC, 1992).

Although this pattern might seem somewhat surprising, as claimed by previous studies, the Natura 2000 network was conceived to protect specific species and habitats listed in the Annexes of the Habitats and Birds directives, highlighting a useful synergy when both directives are congruent. Thus, the potential umbrella effect of the network is conserving more species than those prioritized (Maiorano et al., 2015). Maiorano et al. (2015) highlighted that almost one-third of the EU28 area is under some form of protection when considering both networks, constituting one of the largest continental protected area networks in the world. This network should continuously be updated and protected, given its importance in protecting avian species specialization.

The clumped spatial distribution of all specialization categories indicates the specific environmental requirements of avian specialist species and the essential need for more in-depth knowledge about those environmental characteristics when building protected area systems. Likewise, the spatial congruence between different avian specialization types (here termed multiple hotspots) highlights areas that could represent specific conservation targets. These findings suggest a need to include specialization in conservation planning in regional and European strategies to protect specialized species further. Our results confirm a previous suggestion that the Natura 2000 network indirectly supports the conservation of many specialist species and captures most facets of specialization (Pellissier et al., 2020). Additionally, we show that many types of specialization are spatially congruent, indicating high-interest areas from a conservation perspective. Indeed, nearly 30% of European multiple hotspots are outside the network of protected areas. The Supporting Information (Figure S7) shows two examples of areas potentially demanding higher protection from policy-makers prioritizing conservation efforts. Both examples highlight areas characterized by a high spatial mismatch between specialization hotspots (e.g., single hotspots and multiple hotspots) and Natura 2000 protected areas.

4.4 | Study caveats and future directions

The conservation of ecological specialization could be a potential tool more efficient than species-based approaches because it can filter avian assemblages with characteristics more sensitive to the current environmental change. Although we assessed the extent to which conservation areas intersect with avian specialization richness, richness measures do not incorporate species-specific responses. In future studies, a measure of complementarity would be needed to determine whether the species identified as specialists are being protected equally by the Natura 2000 protected areas in Europe. Additionally, our study provides new insights into the spatial distribution of avian specialization. However, we believe that a deep understanding of the mechanism behind the spatial distribution of avian specialization deserves further studies, preferably by increasing the spatial resolution of the avian distribution data at a local and regional scale. Also, explicit explorations of the mechanisms and causes explaining the spatial distribution of avian specialization, such as vegetation, climate variables and temporal changes in land use or species composition (Araújo et al., 2008; Moura et al., 2016; Trautmann, 2018), not focused on the present study, could contribute to the conservation of the avian specialists (Román-Palacios & Wiens, 2020).

This study used data from the EBCC Atlas of European breeding birds (EBBA1) published in 1997 (Hagemeijer & Blair, 1997), potentially introducing a temporal bias. Thus, considering the relevance of using updated data for conservation planning, when data from the new Atlas (EBBA2) become available (https://www.ebba2.info/what-is-ebba2-and-why-ebba2/), further studies could track changes in avian specialization patterns. Thus, similar approaches to that of the present study could be informative in helping future protected area planning throughout Europe. Furthermore, given that protected areas are crucial for biodiversity conservation (Watson et al., 2014), playing an essential role in climate change mitigation at a global or local scale (Mawdsley et al., 2009), new studies should explore the effects of different climate change scenarios (Morelli et al., 2020) on shaping the spatial distribution of different types of avian specialization in Europe.

4.5 | Conclusions

As conservation knowledge and concerns evolve, a re-evaluation of conservation priorities and priority areas for biodiversity conservation is essential (Jenkins et al., 2013). In this sense, the EU Biodiversity Strategy for 2030 aims to increase the existing European Natura 2000 network (EC, 2020). Accordingly, we suggest: (1) that the prioritization must also be focused on avian specialization because it could be more efficient than species-based approaches, capturing other community attributes more susceptible to land-use or climate changes; (2) considering each category of avian specialization separately because their spatial patterns are different at biogeographical scales; (3) including climate specialization in further studies, considering that climate is the main driver shaping global biodiversity (Román-Palacios & Wiens, 2020; Trautmann, 2018); (4) when possible, using multiple hotspots of avian specialization to identify areas where multifaceted specialization is maximized; and (5) evaluating the spatial distribution of avian specialization at a more detailed spatial scale, even at a regional or local spatial scale. Additionally, we suggest including avian ecological specialization drivers (e.g., elevation and dominant land-use type) and considering the specialization hotspots as a conservation target for strict protection, as defined by the EU Biodiversity Strategy for 2030 (EC, 2020).

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding the publication of this article.

AUTHOR CONTRIBUTIONS

All authors contributed to conceiving the study ideas. Y.B. and F.M. designed the analyses. F.M. created the maps. Y.B. performed the data handling and statistical analyses and led the writing of the paper in collaboration with all authors. All authors have approved the final version.

DATA AVAILABILITY STATEMENT

All raw data that support the findings of this study are directly downloadable online:

1. EBCC Atlas of European Breeding Birds (EBBA1): https://www.gbif.org/dataset/c779b049-28f3-4daf-bbf4-0a40830819b6
2. European elevational gradient: https://www.naturalearthdata.com/downloads/10m-raster-data/10m-cross-blend-hypso/
3. CORINE land cover (CLC): https://land.copernicus.eu/pan-european/corine-land-cover/clc2018

4. Natura 2000 protected areas network: https://www.eea.europa.eu/data-and-maps/data/natura-11
5. Avian specialization indices: https://onlinelibrary.wiley.com/doi/full/10.1002/ece3.5419

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BIOSKETCH

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SUPPORTING INFORMATION

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