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*

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

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 georeferenced 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 re-classified 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
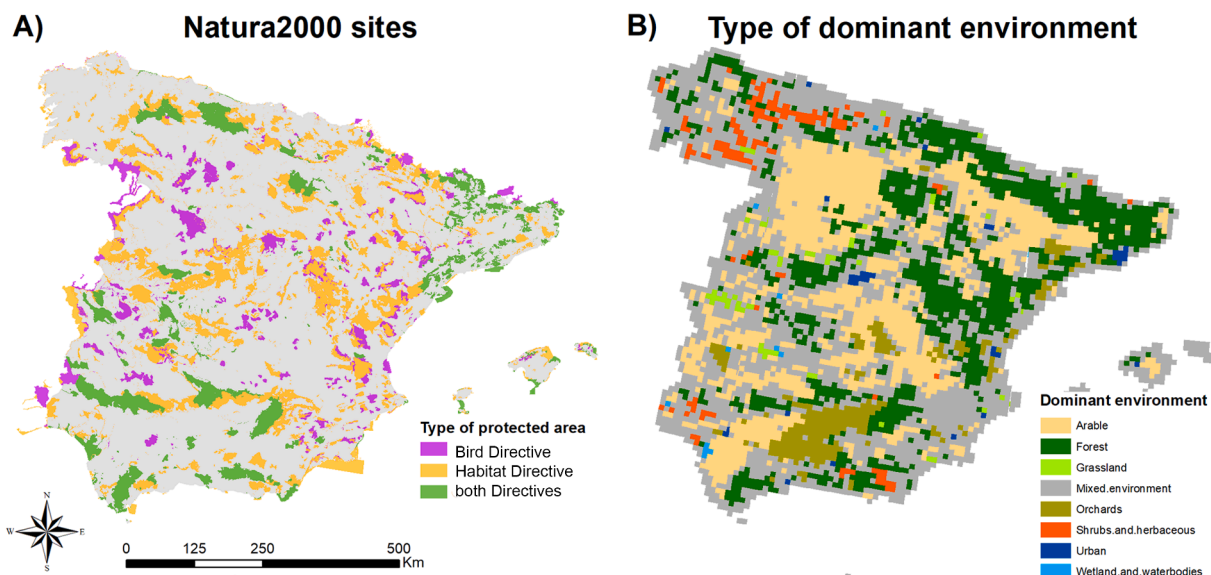

Fig. 1. Types of Natura 2000 areas, based on the category of designation (Birds Directive, Habitat Directive, both Directives) (A) and main types of dominant environments (B) in Spain. The spatial units used for mapping are 10×10 km squares (total number of squares 5,390).

'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).
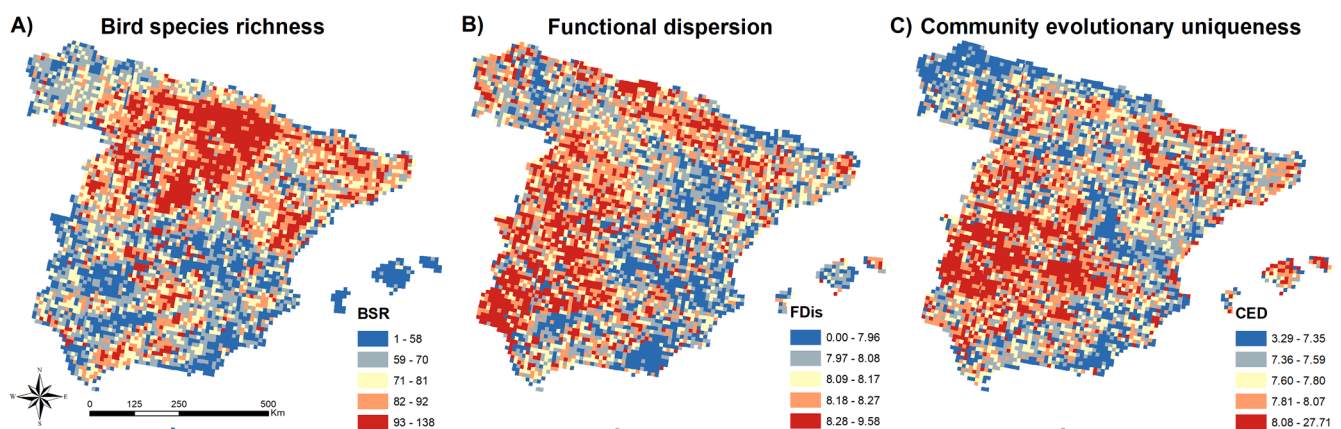

Fig. 2. Spatial distribution of avian diversity in Spain: A) the number of bird species, B) functional dispersion, and C) community evolutionary distinctiveness or uniqueness. The spatial units used for mapping consist of 5,390 cells of 10 × 10 km covering the Spanish territory.

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

Type of environment	Non-PA			<20% PA			Birds Directive			Habitat Directive			Both Directives			Other type			Overall
	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

Type of environment	Non-PA			<20% PA			Birds Directive			Habitat Directive			Both Directives			Other type			Overall
	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

Type of environment	Non-PA			<20% PA			Birds Directive			Habitat Directive			Both Directives			Other type			Overall
	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

5

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

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**

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.

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
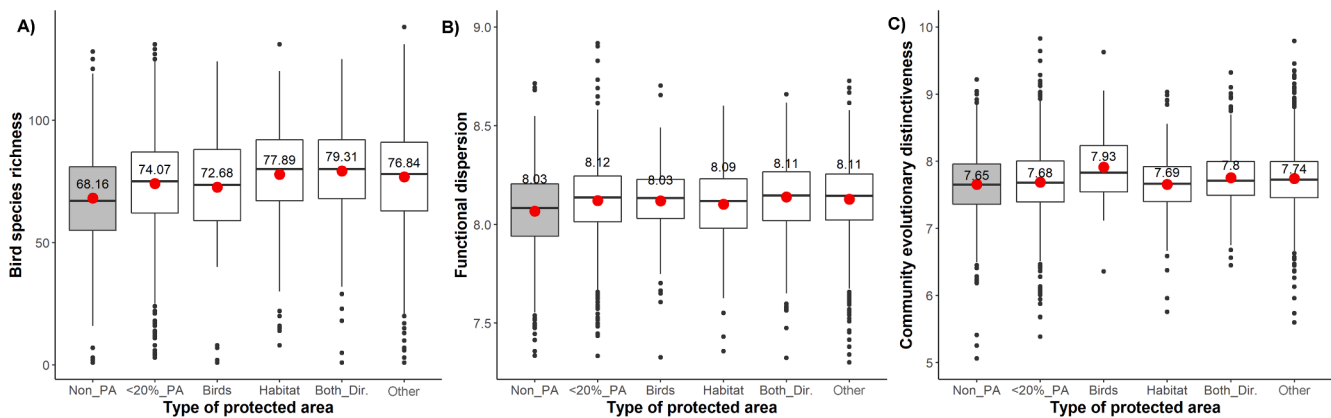
Fig. 3. Box plots of the number of bird species (A), functional dispersion in the avian species assemblage (B) and community evolutionary distinctiveness or uniqueness in each type of protected area (Birds Directive, Habitat Directive, both Directives, other combination types and < 20% covered by protected 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 (EURO-PARC-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.

Acknowledgements

Appendix A. Supplementary data

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

References

Barnard, P., Brown, C.J., Jarvis, A.M., Robertson, A., Rooyen, L.V., 1998. Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. Biodivers. Conserv. 7, 531–547. https://doi.org/10.1023/A:1008831829574.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4 - R Package.

Benedetti, Y., Morelli, F., Munafò, M., Assennato, F., Strollo, A., Santolini, R., 2020. Spatial associations among avian diversity, regulating and provisioning ecosystem services in Italy. Ecol. Indic. 108, 105742. https://doi.org/10.1016/j.ecolind.2019.105742.

Bennett, P.M., Owens, I.P.F., 2002. Evolutionary ecology of birds: life histories, mating systems and extinction. Oxford University Press, Oxford, UK.

Bibby, C.J., Hill, D.A., Burgess, N.D., Mustoe, S., 2000. Bird census techniques, 2nd ed. Academic Press, London, UK.

Bonn, A., Gaston, K.J., 2005. Capturing biodiversity: selecting priority areas for conservation using different criteria. Biodivers. Conserv. 14 (5), 1083–1100. https://doi.org/10.1007/s10531-004-8410-6.

Bossard, M., Feranec, J., Othael, J., 2000. CORINE land cover technical guide – Addendum. European Environment Agency Technical Report 40. Copenhagen.

Butler, S.J., Boccaccio, L., Gregory, R.D., Vorisek, P., Norris, K., 2010. Quantifying the impact of land-use change to European farmland bird populations. Agric. Ecosyst. Environ. 137 (3-4), 348–357. https://doi.org/10.1016/j.agee.2010.03.005.

Cadotte, M.W., Davies, T.J., 2010. Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. Divers. Distrib. 16, 376–385.

Carrascal, L.M., Lobo, J., 2003. Respuestas a viejas preguntas con nuevos datos: estudio de los patrones de distribución de la avifauna española y su aplicación en conservación. In: Martí, R., del Moral, J.C. (Eds.), Atlas de Las Aves Nificantes de España. Sociedad Española de Ornitología, Madrid, España, pp. 651–668.

CBD Secretariat, 2019. Convention on Biological Diversity [WWW Document]. URL https://www.cbd.int/countries/profile/?country=es.

Charbonnier, Y.M., Barbaro, L., Barnagaud, J.-Y., Ampoorter, E., Nezan, J., Verheyen, K., Jactel, H., 2016. Bat and bird diversity along independent gradients of latitude and tree composition in European forests. Oecologia 182 (2), 529–537. https://doi.org/10.1007/s00442-016-3671-9.

Chong, K.Y., Teo, S., Kurukulasuriya, B., Chung, Y.F., Rajathurai, S., Tan, H.T.W., 2014. Not all green is as good: Different effects of the natural and cultivated components of urban vegetation on bird and butterfly diversity. Biol. Conserv. 171, 299–309. https://doi.org/10.1016/j.biocon.2014.01.037.

Clark, C.M., Flynn, D.F.B., Butterfield, B.J., Reich, P.B., Cahill, J.F., 2012. Testing the Link between Functional Diversity and Ecosystem Functioning in a Minnesota Grassland Experiment. PLoS One 7 (12), e52821. https://doi.org/10.1371/journal.pone.005282110.1371/journal.pone.0052821.g00110.1371/journal.pone.0052821.g00210.1371/journal.pone.0052821.g00310.1371/journal.pone.0052821.g00410.1371/journal.pone.0052821.g00510.1371/journal.pone.0052821.t00110.1371/journal.pone.0052821.t00210.1371/journal.pone.0052821.t00310.1371/journal.pone.0052821.t00410.1371/journal.pone.0052821.s00110.1371/journal.pone.0052821.s00210.1371/journal.pone.0052821.s003.

Cooke, R.S.C., Bates, A.E., Eigenbrod, F., Schrodt, F., 2019. Global trade-offs of functional redundancy and functional dispersion for birds and mammals. Glob. Ecol. Biogeogr. 28 (4), 484–495. https://doi.org/10.1111/geb.v28.410.1111/geb.12869.

de Baan, L., Alkemade, R., Koellner, T., 2013. Land use impacts on biodiversity in LCA: A global approach. Int. J. Life Cycle Assess. 18 (6), 1216–1230. https://doi.org/10.1007/s11367-012-0412-0.

de la Concha, I., 2005. The Common Agricultural Policy and the role of Rural Development Programmes in the conservation of steppe birds, in: Lynx Edicions & Centre Tecnològic Forestal de Catalunya, B. (Ed.). In Bota G, Morales MB, Mañosa S, Campro¬don J (Eds). Ecology and Conservation of Steppe-Land Birds. pp. 141–168.

Devictor, Vincent, Julliard, Romain, Couvet, Denis, Lee, Alexandre, Jiguet, Frédéric, 2007. Functional homogenization effect of urbanization on bird communities. Conserv. Biol. 21 (3), 741–751. https://doi.org/10.1111/cbi.2007.21.issue-310.1111/j.1523-1739.2007.00671.x.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345 (6195), 401–406. https://doi.org/10.1126/science:1251817.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I, Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography (Cop.) 30 (5), 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x.

EDGE of Existence, 2015. www.edgeofexistence.org [WWW Document].

Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response Diversity, Ecosystem Change, and Resilience. Front. Ecol. Environ. 1, 488–494. https://doi.org/10.2307/3868116.

ESRI, 2012. ArcGIS Desktop: Release 10.1.

EUROPARC-España, 2019. Anuario 2018 del estado de las áreas protegidas en España. Fundación Fernando González Bernáldez, Madrid, España.

European Environment Agency, 2019. Natura 2000 data - the European network of protected sites.

European Environment Agency (EEA), Copernicus programme, 2018. Corine Land Cover (CLC) [WWW Document]. Version 20. URL https://land.copernicus.eu/pan-european/corine-land-cover/clc2018.

Eurostat, 2021. Natura 2000 protected areas [WWW Document]. Data Brows. https://ec.europa.eu/eurostat/databrowser/view/env_bio1/default/table?lang=en.

Evans, Douglas, 2012. Building the European Union's Natura 2000 network. Nat. Conserv. 1, 11–26.

Evans, M.I., Heath, M.F., 2000. Important Bird Areas in Europe. Southern Europe. Birdlife International.

Faith, Daniel P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61 (1), 1–10. https://doi.org/10.1016/0006-3207(92)91201-3.

Fleishman, E., Noss, R., Noon, B., 2006. Utility and limitations of species richness metrics for conservation planning. Ecol. Indic. 6 (3), 543–553. https://doi.org/10.1016/j.ecolind.2005.07.005.

Frishkoff, L.O., Karp, D.S., M'Gonigle, L.K., Mendenhall, C.D., Zook, J., Kremen, C., Hadly, E.A., Daily, G.C., 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. Science 345, 1343–1346. https://doi.org/10.7910/DVN/26910.

Fuller, Richard A., McDonald-Madden, Eve, Wilson, Kerrie A., Carwardine, Josie, Grantham, Hedley S., Watson, James E.M., Klein, Carissa J., Green, David C., Possingham, Hugh P., 2010. Replacing underperforming protected areas achieves better conservation outcomes. Nature 466 (7304), 365–367. https://doi.org/10.1038/nature09180.

Gaston, Kevin J., Jackson, Sarah F., Cantú-Salazar, Lisette, Cruz-Piñón, Gabriela, 2008. The Ecological Performance of Protected Areas. Annu. Rev. Ecol. Evol. Syst. 39 (1), 93–113. https://doi.org/10.1146/ecolsys.2008.39.issue-110.1146/annurev.ecolsys.39.110707.173529.

Gaüzère, Pierre, Jiguet, Frédéric, Devictor, Vincent, Loyola, Rafael, 2016. Can protected areas mitigate the impacts of climate change on bird's species and communities? Divers. Distrib. 22 (6), 625–637. https://doi.org/10.1111/ddi.2016.22.issue-610.1111/ddi.12426.

Gerisch, Michael, Agostinelli, Veronica, Henle, Klaus, Dziock, Frank, 2012. More species, but all do the same: Contrasting effects of flood disturbance on ground beetle functional and species diversity. Oikos 121 (4), 508–515. https://doi.org/10.1111/more.2012.121.issue-410.1111/j.1600-0706.2011.19749.x.

Goded, Sandra, Ekroos, Johan, Domínguez, Jesús, Azcárate, Joaquín G., Guitián, José A., Smith, Henrik G., 2019. Effects of eucalyptus plantations on avian and herb species richness and composition in North-West Spain. Glob. Ecol. Conserv. 19, e00690. https://doi.org/10.1016/j.gecco.2019.e00690.

González-Taboada, F., Nores, C., Álvarez, M.Á., 2007. Breeding bird species richness in Spain: Assessing diversity hypothesis at various scales. Ecography (Cop.) 30, 241–250. https://doi.org/10.1111/j.2007.0906-7590.04824.x.

Gregory, Richard D., Gibbons, David W., Donald, Paul F., 2004. In: Bird Ecology and Conservation. Oxford University Press, pp. 17–56. https://doi.org/10.1093/acprof:oso/9780198520863.003.0002.

Heath, M.F., Evans, M.I., Hoccom, D.G., Payne, A.J., Peet, N.B., 2000. Important Bird Areas in Europe: priority sites for conservation. Volume 1: Northern Europe, Volume 2: Southern Europe. In: Heath, M.F., Evans, M.I., Hoccom, D.G., Payne, A.J., Peet, N.B. (Eds.), Important Bird Areas in Europe: Priority Sites for Conservation. BirdLife International, Cambridge, UK, p. 804.

Hoffmann, S., Beierkuhnlein, C., Field, R., Provenzale, A., Chiarucci, A., 2018. Uniqueness of protected areas for conservation strategies in the European Union. Sci. Rep. 8, 1–14. https://doi.org/10.1038/s41598-018-24390-3.

Hui, Cang, McGeoch, Melodie A., 2014. Zeta diversity as a concept and metric that unifies incidence-based biodiversity patterns. Am. Nat. 184 (5), 684–694. https://doi.org/10.1086/678125.

Ibáñez-Álamo, Juan Diego, Rubio, Enrique, Benedetti, Yanina, Morelli, Federico, 2017. Global loss of avian evolutionary uniqueness in urban areas. Glob. Chang. Biol. 23 (8), 2990–2998. https://doi.org/10.1111/gcb.2017.23.issue-810.1111/gcb.13567.

Isaac, Nick J.B., Turvey, Samuel T., Collen, Ben, Waterman, Carly, Baillie, Jonathan E.M., Reid, Walt, 2007. Mammals on the EDGE: conservation priorities based on threat and phylogeny. PLoS One 2 (3), e296. https://doi.org/10.1371/journal.pone.000029610.1371/journal.pone.0000296.g00110.1371/journal.pone.0000296.g00210.1371/journal.pone.0000296.g00310.1371/journal.pone.0000296.s00110.1371/journal.pone.0000296.s002.

Jetz, W., Thomas, G.H.H., Joy, J.B.B., Redding, D.W.W., Hartmann, K., Mooers, A.O.Ø., 2014. Global Distribution and Conservation of Evolutionary Distinctness in Birds. Curr. Biol. 24, 919–930. doi:10.1016/j.cub.2014.03.011.

Kukkala, A.S., Arponen, A., Maiorano, L., Moilanen, A., Thuiller, W., Toivonen, T., Zupan, L., Brotons, L., Cabeza, M., 2016. Matches and mismatches between national and EU-wide priorities: Examining the Natura 2000 network in vertebrate species conservation. Biol. Conserv. 198, 193–201. https://doi.org/10.1016/j.biocon.2016.04.016.

Lai, Shu-Mei, Liu, Wei-Chung, Jordán, Ferenc, 2012. On the centrality and uniqueness of species from the network perspective. Biol. Lett. 8 (4), 570–573. https://doi.org/10.1098/rsbl.2011.1167.

Laliberté, Etienne, Legendre, Pierre, 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91 (1), 299–305. https://doi.org/10.1890/08-2244.1.

Laliberté, E., Legendre, P., Shipley, B., 2015. Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology: R package version 1.0-12.

Lascelles, B.G., Langham, G.M., Ronconi, R.A., Reid, J.B., 2012. From hotspots to site protection: Identifying Marine Protected Areas for seabirds around the globe. Biol. Conserv. 156, 5–14. https://doi.org/10.1016/j.biocon.2011.12.008.

Laureto, Livia Maira Orlandi, Cianciaruso, Marcus Vinicius, Samia, Diogo Soares Menezes, 2015. Functional diversity: An overview of its history and applicability. Nat. e Conserv. 13 (2), 112–116. https://doi.org/10.1016/j.ncon.2015.11.001.

Legendre, P., Fortin, M.-J., 2010. Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. Mol. Ecol. Resour. 10, 831–844. https://doi.org/10.1111/j.1755-0998.2010.02866.x.

Lombard, A.T., 1995. The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? South African. J. Zool. 30 (3), 145–163. https://doi.org/10.1080/02541858.1995.11448382.

Maes, Dirk, Bauwens, Dirk, De Bruyn, Luc, Anselin, Anny, Vermeersch, Glenn, Van Landuyt, Wouter, De Knijf, Geert, Gilbert, Marius, 2005. Species richness coincidence: conservation strategies based on predictive modelling. Biodivers. Conserv. 14 (6), 1345–1364. https://doi.org/10.1007/s10531-004-9662-x.

Magurran, A., 2004. Measuring Biological Diversity. Blackwell Science, Oxford, UK.

Manolache, S., Nita, A., Ciocanea, C.M., Popescu, V.D., Rozylowicz, L., 2018. Power, influence and structure in Natura 2000 governance networks. A comparative analysis of two protected areas in Romania. J. Environ. Manage. 212, 54–64. https://doi.org/10.1016/j.jenvman.2018.01.076.

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

Margules, C.R., Pressey, R.L., Williams, P.H., 2002. Representing biodiversity: Data and procedures for identifying priority areas for conservation. J. Biosci. 27 (4), 309–326. https://doi.org/10.1007/BF02704962.

Martí, R., Del Moral, J.C., 2003. Atlas de las Aves Reproductoras de España. Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología, Madrid, España.

Mason, Norman W.H., de Bello, Francesco, Mouillot, David, Pavoine, Sandrine, Dray, Stéphane, Zobel, Martin, 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. J. Veg. Sci. 24 (5), 794–806. https://doi.org/10.1111/jvs.12013.

Medail, Frederic, Quezel, Pierre, 1999. Biodiversity hotspots in the Mediterranean Basin: Setting global conservation priorities. Conserv. Biol. 13 (6), 1510–1513. https://doi.org/10.1046/j.1523-1739.1999.98467.x.

Mitchell, B., Stolton, S., Bezaury-Creel, J., Bingham, H., Cumming, T., Dudley, N., Fitzsimons, J., Malleret-King, D., Redford, K., Solano, P., 2018. Guidelines for privately protected areas, Best Practice Protected Area Guidelines Series No. 29. Gland, Switzerland. doi:10.2305/iucn.ch.2018.pag.29.en.

Mittermeier, R.A., Robles Gil, P., Hoffman, M., Pilgrim, J., Brooks, T., Goettsch Mittermeier, C., Lamoreux, J., da Fonseca, G.A.B., Seligmann, P.A., Ford, H., 2005. Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. Conservation International.

Morelli, Federico, 2015. Indicator species for avian biodiversity hotspots: combination of specialists and generalists is necessary in less natural environments. J. Nat. Conserv. 27, 54–62.

Morelli, Federico, Benedetti, Yanina, Ibáñez-Álamo, Juan Diego, Jokimäki, Jukka, Mänd, Raivo, Tryjanowski, Piotr, Møller, Anders Pape, 2016. Evidence of evolutionary homogenization of bird communities in urban environments across Europe. Glob. Ecol. Biogeogr. 25 (11), 1284–1293. https://doi.org/10.1111/geb.12486.

Morelli, F., Benedetti, Y., Perna, P., Santolini, R., 2018. Associations among taxonomic diversity, functional diversity and evolutionary distinctiveness vary among environments. Ecol. Indic. 88, 8–16. https://doi.org/10.1016/j.ecolind.2018.01.022.

Morelli, F., Benedetti, Y., Su, T., Zhou, B., Moravec, D., Šímová, P., Liang, W., 2017. Taxonomic diversity, functional diversity and evolutionary uniqueness in bird communities of Beijing's urban parks: effects of land use and vegetation structure. Urban For. Urban Green. 23, 84–92. https://doi.org/10.1016/j.ufug.2017.03.009.

Morelli, Federico, Møller, Anders Pape, 2018. Pattern of evolutionarily distinct species among four classes of animals and their conservation status: a comparison using evolutionary distinctiveness scores. Biodivers. Conserv. 27 (2), 381–394. https://doi.org/10.1007/s10531-017-1441-6.

Morelli, F., Pruscini, F., Santolini, R., Perna, P., Benedetti, Y., Sisti, D., 2013. Landscape heterogeneity metrics as indicators of bird diversity: Determining the optimal spatial scales in different landscapes. Ecol. Indic. 34, 372–379. https://doi.org/10.1016/j.ecolind.2013.05.021.

Múgica de la Guerra, M., Martínez Alandi, C., Puertas Blázquez, J., Atauri Mezquida, J. A., Gómez-Limón García, J., García Ventura, D., 2019. Anuario 2018 del estado de las áreas protegidas en España.

Myers, Norman, Mittermeier, Russell A., Mittermeier, Cristina G., da Fonseca, Gustavo A. B., Kent, Jennifer, 2000. Biodiversity hotspots for conservation priorities. Nature 403 (6772), 853–858. https://doi.org/10.1038/35002501.

Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, B.R., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. vegan: Community Ecology Package. R package version 2.3-4.

Pascual, López-López, Luigi, Maiorano, Alessandra, Falcucci, Emilio, Barba, Luigi, Boitani, 2011. Hotspots of species richness, threat and endemism for terrestrial vertebrates in SW Europe. Acta Oecologica 37 (5), 399–412. https://doi.org/10.1016/j.actao.2011.05.004.

Pautasso, M., Dinetti, M., 2009. Avian species richness, human population and protected areas across Italy's regions. Environ. Conserv. 36, 22–31. https://doi.org/10.1017/S037689290900544X.

Pearman, P.B., Lavergne, S., Roquet, C., Wüest, R., Zimmermann, N.E., Thuiller, W., 2014. Phylogenetic patterns of climatic, habitat and trophic niches in a European avian assemblage. Glob. Ecol. Biogeogr. 23, 414–424. https://doi.org/10.1111/geb.12127.

Petchey, Owen L., Gaston, Kevin J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5 (3), 402–411. https://doi.org/10.1046/j.1461-0248.2002.00339.x.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., R Core Team, 2019. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-140.

R Development Core Team, 2019. R: A language and environment for statistical computing.

Redding, D.W., Dewolff, C.V., Mooers, A.Ø., 2010. Evolutionary distinctiveness, threat status, and ecological oddity in primates. Conserv. Biol. 24, 1052–1058. https://doi.org/10.1111/j.1523-1739.2010.01532.x.

Redding, David W., Mooers, Arne O., Şekercioğlu, Çağan H., Collen, Ben, 2015. Global evolutionary isolation measures can capture key local conservation species in Nearctic and Neotropical bird communities. Philos. Trans. R. Soc. London B - Biol. Sci. 370 (1662), 20140013. https://doi.org/10.1098/rstb.2014.0013.

Ricotta, Carlo, Moretti, Marco, 2011. CWM and Rao's quadratic diversity: A unified framework for functional ecology. Oecologia 167 (1), 181–188. https://doi.org/10.1007/s00442-011-1965-5.

Rodrigues, A.S.L., Akçakaya, H.R., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Chanson, J.S., Fishpool, L.D.C., Da Fonseca, G.a.B., Gaston, K.J., Hoffmann, M., Marquet, P.a., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004. Global Gap Analysis: Priority Regions for Expanding the Global Protected-Area Network. Bioscience 54, 1092–1100. https://doi.org/10.1641/0006-3568(2004)054[1092:GGAPRF]2.0.CO;2.

Rodrigues, A.S.L.L., Brooks, T.M., Rodrigues, A.S.L.L., Brooks, T.M., 2007. Shortcuts for Biodiversity Conservation Planning : The Effectiveness of Surrogates. Annu. Rev. Ecol. Evol. Syst. 38, 713–737. https://doi.org/10.1146/annurev.ecolsys.38.091206.095737.

Rodriguez-Rodriguez, D., Lopez, I., 2018. Effects of legal designation and management of a multiple-use protected area on local sustainability. Sustainability 10, 3176. doi:10.3390/su10093176.

Safi, Kamran, Armour-Marshall, Katrina, Baillie, Jonathan E.M., Isaac, Nick J.B., Davies, Zoe G., 2013. Global Patterns of Evolutionary Distinct and Globally Endangered Amphibians and Mammals. PLoS One 8 (5), e63582. https://doi.org/10.1371/journal.pone.006358210.1371/journal.pone.0063582.g00110.1371/journal.pone.0063582.g00210.1371/journal.pone.0063582.g00310.1371/journal.pone.0063582.t00110.1371/journal.pone.0063582.t00210.1371/journal.pone.0063582.s00110.1371/journal.pone.0063582.s00210.1371/journal.pone.0063582.s00310.1371/journal.pone.0063582.s00410.1371/journal.pone.0063582.s00510.1371/journal.pone.0063582.s00610.1371/journal.pone.0063582.s00710.1371/journal.pone.0063582.s00810.1371/journal.pone.0063582.s009.

Schröter, Matthias, Remme, Roy P., 2016. Spatial prioritisation for conserving ecosystem services: comparing hotspots with heuristic optimisation. Landsc. Ecol. 31 (2), 431–450. https://doi.org/10.1007/s10980-015-0258-5.

Sekercioglu, C., 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21 (8), 464–471. https://doi.org/10.1016/j.tree.2006.05.007.

Seymour, Colleen L., Simmons, Robert E., Joseph, Grant S., Slingsby, Jasper A., 2015. On Bird Functional Diversity: Species Richness and Functional Differentiation Show Contrasting Responses to Rainfall and Vegetation Structure in an Arid Landscape. Ecosystems 18 (6), 971–984. https://doi.org/10.1007/s10021-015-9875-8.

Sol, Daniel, Bartomeus, Ignasi, González-Lagos, César, Pavoine, Sandrine, Haddad, Nick, 2017. Urbanisation and the loss of phylogenetic diversity in birds. Ecol. Lett. 20 (6), 721–729. https://doi.org/10.1111/ele.2017.20.issue-610.1111/ele.12769.

Thompson, Patrick L., Davies, T. Jonathan, Gonzalez, Andrew, Liang, Wenju, 2015. Ecosystem functions across trophic levels are linked to functional and phylogenetic diversity. PLoS One 10 (2), e0117595. https://doi.org/10.1371/journal.pone.011759510.1371/journal.pone.0117595.g00110.1371/journal.pone.0117595.g00210.1371/journal.pone.0117595.g00310.1371/journal.pone.0117595.t00110.1371/journal.pone.0117595.t00210.1371/journal.pone.0117595.s00110.1371/journal.pone.0117595.s00210.1371/journal.pone.0117595.s00310.1371/journal.pone.0117595.s00410.1371/journal.pone.0117595.s00510.1371/journal.pone.0117595.s00610.1371/journal.pone.0117595.s00710.1371/journal.pone.0117595.s00810.1371/journal.pone.0117595.s00910.1371/journal.pone.0117595.s010.

Tribot, A.-S., Mouquet, N., Villéger, S., Raymond, M., Hoff, F., Boissery, P., Holon, F., Deter, J., 2016. Taxonomic and functional diversity increase the aesthetic value of coralligenous reefs. Sci. Rep. 6, 34229. https://doi.org/10.1038/srep34229.

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

Tucker, Caroline M., Cadotte, Marc W., Carvalho, Silvia B., Davies, T. Jonathan, Ferrier, Simon, Fritz, Susanne A., Grenyer, Rich, Helmus, Matthew R., Jin, Lanna S., Mooers, Arne O., Pavoine, Sandrine, Purschke, Oliver, Redding, David W., Rosauer, Dan F., Winter, Marten, Mazel, Florent, 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biol. Rev. 92 (2), 698–715. https://doi.org/10.1111/brv.12252.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, 4th ed. Springer, New York. doi:10.1007/978-0-387-21706-2.

Venter, Oscar, Fuller, Richard A., Segan, Daniel B., Carwardine, Josie, Brooks, Thomas, Butchart, Stuart H.M., Di Marco, Moreno, Iwamura, Takuya, Joseph, Liana, O'Grady, Damien, Possingham, Hugh P., Rondinini, Carlo, Smith, Robert J., Venter, Michelle, Watson, James E.M., Moritz, Craig, 2014. Targeting global protected area expansion for imperiled biodiversity. PLoS Biol. 12 (6), e1001891. https://doi.org/10.1371/journal.pbio.100189110.1371/journal.pbio.1001891.g00110.1371/journal.pbio.1001891.g00210.1371/journal.pbio.1001891.g00310.1371/journal.pbio.1001891.t00110.1371/journal.pbio.1001891.s00110.1371/journal.pbio.1001891.s00210.1371/journal.pbio.1001891.s00310.1371/journal.pbio.1001891.s004.

Villéger, Sébastien, Mason, Norman W.H., Mouillot, David, 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89 (8), 2290–2301. https://doi.org/10.1890/07-1206.1.

Villéger, S., Miranda, J.R., Hernandez, D.F., Mouillot, D., 2012. Low functional diversity despite high taxonomic diversity among tropical estuarine fish communities. PLoS One 7, e40679. https://doi.org/10.1371/journal.pone.0040679.

Wiens, J.A., Hayward, G.D., Holthausen, R.S., Wisdom, M.J., 2008. Using Surrogate Species and Groups for Conservation Planning and Management. Bioscience 58, 241–252. https://doi.org/10.1641/B580310.

Young, Juliette, Watt, Allan, Nowicki, Peter, Alard, Didier, Clitherow, Jeremy, Henle, Klaus, Johnson, Richard, Laczko, Endre, McCracken, Davy, Matouch, Simone, Niemela, Jari, Richards, Caspian, 2005. Towards sustainable land use: Identifying and managing the conflicts between human activities and biodiversity conservation in Europe. Biodivers. Conserv. 14 (7), 1641–1661. https://doi.org/10.1007/s10531-004-0536-z.