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Coverage of vertebrate species distributions by Important Bird and Biodiversity Areas and Special Protection Areas in the European Union

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ABSTRACT

The European Union (EU) has an extensive protected area network, including Special Protection Areas (SPAs) designated under the Birds Directive. Important Bird and Biodiversity Areas (IBAs) are sites of international significance for birds identified by BirdLife International. Here, we perform EU-wide terrestrial spatial conservation prioritizations to evaluate the coverage of IBAs by SPAs, and the coverage of bird and other vertebrate distributions by IBAs and SPAs. We then investigate the distribution of potential locations for expanding the SPA network that maximize bird species' representation, and the coverage of these locations by IBAs. On average, SPAs cover 23% of the EU-wide distribution of each bird species and 25% of the distributions of amphibians, reptiles and mammals together, while IBAs provide marginally greater coverage. Overall, 76% of terrestrial IBAs in the EU are completely or partially covered by SPAs, and 66% of the IBA network area is covered by SPAs. Our results suggest that SPA designation has been significantly informed by data on the location of IBAs. While IBAs are identified using data on particular bird species of conservation concern, they also tend to have high EU-wide representation of other vertebrates. The designation of new or expanded SPAs covering a relatively small amount of currently unprotected land (particularly in the southern EU) would substantially increase SPA coverage of bird species ranges. Our analysis provides insights on the current contribution that these sites make to conserving vertebrates across the EU, and future possibilities for efficiently expanding the network.

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1. Introduction

In Europe, one of the oldest policy tools for bird conservation is the 1979 European Union (EU) Birds Directive (2009/147/EC), which covers all naturally occurring wild bird species in the EU (European Commission, 2015a). One of its aims is to conserve the habitats of particularly threatened species (listed on Annex I) and migratory species by designating key sites as Special Protection Areas (SPAs). Along with Sites of Community Interest (SCIs) designated as Special Areas for Conservation (SACs) for other taxa and habitats under the 1992 EU Habitats Directive (92/43/EEC; European Commission, 2015b), SPAs form the

EU-wide Natura 2000 network of protected sites, which is at the core of the EU's biodiversity strategy (European Commission, 2011). Site selection for Natura 2000 has been a process guided by the European Commission and implemented in collaboration with the 28 EU Member States (Evans, 2012; European Commission, 2015a, 2015b).

Important Bird and Biodiversity Areas (IBAs) are sites of international significance for bird conservation. Worldwide, >12,000 IBAs have been identified by the BirdLife International Partnership, using standardized data-driven selection criteria based on threat and irreplaceability (Fishpool et al., 1998; BirdLife International, 2011, 2014). In Europe, 20 criteria with different numerical thresholds have been used to identify IBAs of global (A), European (B) and EU (C) significance (Heath and Evans, 2000). The latter were developed and applied explicitly to identify sites qualifying for designation as SPAs, and the IBA inventories listing them have been recognized as providing the best available scientific evidence by the European Court of Justice in several cases brought against Member States for failure to designate sufficient SPAs (e.g. Case C-3/96, Case C-202/01, Stroud, 2011; Evans, 2012; BirdLife International 2013,

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2014). By 2013, two thirds of the terrestrial area of IBAs in the EU had been designated as SPAs (BirdLife International, 2013).

Protected areas are an effective tool for biodiversity conservation worldwide, and many species are highly dependent on them for their persistence (Watson et al., 2014). However, many protected areas have been designated based on little data on biodiversity, or using information on a limited number of taxa (Rodrigues and Brooks, 2007), often leading to a situation where species are only protected coincidentally, rather than intentionally. Birds are known to be useful surrogates for other biodiversity in many cases, and their protection is expected to provide benefits to other taxa (Roberge and Angelstam, 2004; Gregory et al., 2005; Larsen et al., 2012). IBAs have been shown to be important sites for non-avian taxa as well (Brooks et al., 2001; O'Dea et al., 2006; Butchart et al., 2012, 2015; Di Marco et al., 2015).

While the effectiveness of protected areas varies, knowing how well species are covered by protected areas is key to understanding the network's potential impact. Due to increases in available data, spatial conservation prioritization tools have become more common in investigating species coverage by protected areas (Pouzols et al., 2014). While linking to systematic conservation planning (SCP; Margules and Pressey, 2000) and accounting for complementarity, spatial prioritization can be used, for example, to identify spatial priorities, identify locations important for expanding current protected area networks, and understand species' coverage by protected areas.

A number of studies have demonstrated the effectiveness of the Birds Directive and SPAs in conserving wild birds in the EU (Donald et al., 2007; Devictor et al., 2007; Pellissier et al., 2013; Kolecek et al., 2014; EEA, 2015a; Sanderson et al., 2015; Beresford et al., 2016). Nevertheless, other studies have suggested that current SPAs are insufficient to conserve particular species in the EU (Lopez-Lopez et al., 2007; Abellán et al., 2011; Albuquerque et al., 2013; Van der Vliet et al., 2015). Thus, the adequacy and comprehensiveness of the SPA network remains partly unclear. In February 2014, the European Commission received a mandate to deliver a "Fitness Check" of the Birds and Habitats Directives as part of the Commission's Regulatory Fitness and Performance program (REFIT), aiming at simplifying EU law (European Commission, 2014, 2015c). This exercise confirmed the need to assess the relevance and coherence of the Birds Directive.

Here we combine spatial datasets on SPAs and IBAs with high-resolution vertebrate species' distribution maps (Maiorano et al., 2013). We then analyze these data within a complementarity-based spatial conservation prioritization method (Moilanen et al., 2005). The general aim of this study is to investigate the coverage that the IBA and SPA networks provide to birds and other vertebrates, across the EU and at Member State level, considering the overall representativeness (i.e. the average proportion of species' distributions covered in a network).

Specifically, we first aim to quantify the spatial overlap between SPAs and IBAs, and infer how well IBAs have served to inform the designation of SPAs. Second, we investigate the representativeness of SPAs and IBAs in covering the distributions of birds as compared with other vertebrates within the EU. Third, as these networks may undergo site additions or revisions in the future, e.g. in light of international agreements such as the Convention on Biological Diversity (CBD, 2015) Aichi Target 11 to protect 17% of land, we aim to identify unprotected areas that could be incorporated into an expanded SPA network to efficiently increase coverage of species. In doing so, we also assess the extent to which such potential expansion sites have already been identified as IBAs. Such assessments have not previously been done systematically, and they can provide valuable information for decision-makers.

2. Materials and methods

2.1. Study region and data

SPAs are designated only within the EU, and the process of establishing them at sea is still underway, so we restricted our analysis to the

terrestrial area of the EU28 Member States. The vertebrate data used as the input for spatial prioritization were species-specific expert-based distribution models over the Western Palearctic, available for 435 birds (including 181 species on Annex I of the Birds Directive), 85 amphibians, 138 reptiles and 179 mammals (Maiorano et al., 2013; see the full list of species in Appendix A). Known ecological habitat requirements were used to refine species distributions via an expert-based modeling approach to produce a map for each species at 300 m resolution, with each pixel classified as suitable habitat (1) or not (0). Finally, the models were validated using randomizations and known points of presence (Maiorano et al., 2013). For computational feasibility, we aggregated the datasets to a 1.5 km resolution by summing the number of suitable 300 m pixels within each 1.5 km pixel, resulting in pixel suitability values between 0 and 25. The same distribution models have been used in similar studies (Maiorano et al., 2013, 2015; Thuiller et al., 2015).

We rasterized the polygons of all terrestrial SPAs (EEA, 2015b) and IBAs in the EU (BirdLife International, 2015a) to the same extent and resolution as the species data. All datasets were rasterized by using the cell centre method in ArcGIS 10.2.

2.2. Spatial conservation prioritizations

We carried out the spatial prioritizations using Zonation v4 (Moilanen et al., 2014). Zonation is software for ecologically-based land-use planning, and it produces a complementarity-based prioritization across the landscape based on the distributions of biodiversity features and optional data such as costs and connectivity. Zonation ranks cells by iteratively removing (ranking) the least valuable remaining cell until the complete landscape has been prioritized (Moilanen et al., 2005; Lehtomäki and Moilanen, 2013). Occurrence levels of features are tracked through the prioritization, which allows maintenance of balance (complementarity) through the ranking, as features that have lost comparatively much rise in their importance. Across all runs, we used the core area method (CAZ; Moilanen et al., 2005, 2014), which bases ranking on the most important occurrence of a (biodiversity) feature in a grid cell, identifying high-priority areas that include high-quality locations for all features, even those that occur in otherwise feature-poor areas. CAZ is a particularly appropriate method for spatial prioritization when data are available for all species of (conservation) interest across the study area (Moilanen et al., 2005), such as is the case in our study.

We started with an EU-wide spatial prioritization where all bird species in our dataset were considered (Appendix A). Second, we included only amphibians, mammals and reptiles, and finally we included all vertebrate species together (Table B.1). We applied a hierarchical prioritization in Zonation for SPAs with a mask raster file for SPAs. In hierarchical prioritization, all the cells are first ranked from the surrounding area of SPAs, and after that Zonation ranks cells within the SPAs (Lehtomäki et al., 2009; Table B.1). In general, this method allows for a gap analysis and optimal expansion of an existing protected area network, and for comparison between the coverage of species' ranges in different networks, such as SPAs or IBAs. We used different GIS layers to focus the hierarchical prioritizations on: i) all SPAs, ii) all IBAs, iii) areas where SPAs and IBAs overlap, and iv) areas covered by IBAs but not SPAs.

Priority areas for a hypothetical expansion of the current SPA network were also identified by the hierarchical analysis in Zonation. Top-priority cells outside the protected areas (i.e. SPAs) are the ones that most rapidly increase aggregate species coverage and representation in the network. EU Member States have committed through CBD Aichi Target 11 to protect at least 17% of their terrestrial and inland water areas, particularly those of importance for biodiversity, by 2020. Hence, we assessed the expansion of terrestrial SPAs from the current 12.5% to cover a theoretical 17% of the EU. A similar approach was also used by Pouzols et al. (2014) to investigate the potential of expanding the global protected area network.

2.3. Post-processing analyses

The first main output of a Zonation analysis is a raster file, representing the ranking of the landscape in terms of conservation priority. A unique priority rank value (from 0.0 to 1.0) is assigned to each individual $1.5 \text{ km} \times 1.5 \text{ km}$ pixel in the prioritization result map. The spatial allocations of cells that maximized coverage of species for birds versus all vertebrate taxa were compared using ArcGIS. To do this, and following Aichi Target 11, we extracted the top 17% of cells from the prioritization maps. Then, we explored the locations of SPAs and IBAs across the EU, and assessed by how much they overlap with these cells that maximized coverage of species (Table B.1). In this context, mean rank values for SPA and IBA networks were extracted from priority rank maps for birds and for all taxa. In addition, we compared Member State specific mean rank values using Zonal Statistics tools in ArcGIS. For the SPA expansion analysis, we extracted the top 4.5% priority cells outside SPAs to detect the spatial pattern of extension locations.

Sites qualify as IBAs if they meet at least one of a standardized set of criteria (Heath and Evans, 2000), while SPAs are designated for species

Table 1

Information on Special Protection Areas (SPAs) as part of the Natura 2000 network in the European Union (EU) and Important Bird and Biodiversity Areas (IBAs) identified by BirdLife International.

	Special Protection Areas (SPAs)	Important Bird and Biodiversity Areas (IBAs)
Extent	European Union	Global
Establisher	European Union	BirdLife International
Initiated	1979 (Birds Directive 79/409/EEC)	Late 1970s
Target	Protection for all wild bird species naturally occurring in the European Union The directive emphasizes also the protection of habitats for endangered as well as migratory species (listed in Annex I), especially through the establishment of a network of Special Protection Areas (SPAs) comprising all of the most suitable territories for these species.	Identification of a network of sites of international importance for birds, defined across the geographical range of those bird species for which a site-based approach is appropriate, to ensure the long-term viability of naturally-occurring bird populations
Sites	5491 sites in the EU including 5286 terrestrial sites (European Commission, 2013; Natura Barometer 2013)	Over 12,000 sites globally (BirdLife International, 2013, 2015b)
Criteria	Article 4.1: Member States shall classify in particular the most suitable territories in number and size as special protection areas for the conservation of these species (Annex I). Article 4.2: Member States shall take similar measures for regularly occurring migratory species not listed in Annex I. SPAs are selected and designated by the Member States with no agreed common EU criteria for site selection. Several countries have used criteria based on the Ramsar 1% of flyway population. Once SPA sites have been designated, site details are forwarded to the European Commission using an agreed format, 'Standard Data Forms'. These forms include general information on the site together with information on the species present. (Evans, 2012, European Commission, 2015a)	Twenty IBA criteria have been developed for the selection of IBAs in Europe. These allow the identification of IBAs, based on a site's international importance for: <ul style="list-style-type: none">• Threatened bird species• Congregatory bird species• Assemblages of restricted-range bird species• Assemblages of biome-restricted bird species Criteria have been developed such that, by applying different ('staggered') numerical thresholds, the international importance of a site for a species may be categorized at three distinct geographical levels: <ul style="list-style-type: none">• Global ('A' criteria)• European ('B' criteria)• European Union ('C' criteria) (Heath and Evans, 2000, BirdLife International, 2013, 2015b, 2016)

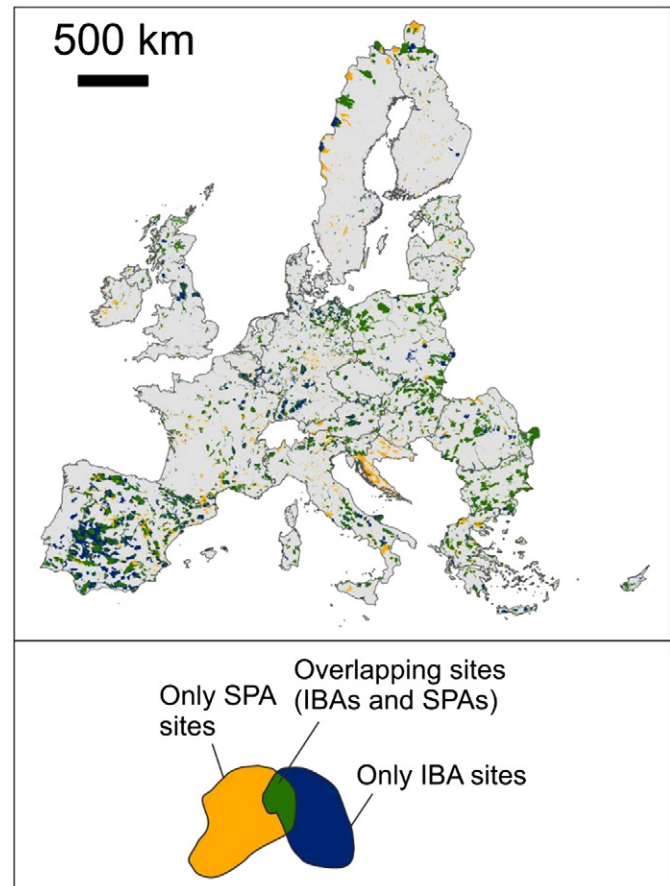


Fig. 1. EU networks of Special Protection Areas (SPAs, shown in orange) defined in the Birds Directive, and Important Bird and Biodiversity Areas (IBAs, shown in blue) identified by BirdLife International. Areas covered by both SPAs and IBAs are shown in green.

listed on Annex I of the Birds Directive and other regularly occurring migrants (Table 1). We explored how well these two networks cover the distributions of bird species and other terrestrial vertebrate species in the EU. We extracted this information for all species from the “performance curves”, which is the second main output of Zonation. These curves report the remaining proportion of a species' range across all stages of the landscape ranking. The performance curves for each species can be examined at the known extent of SPAs, which directly tells the fraction of its distribution inside SPAs (e.g. within the top 12.5% of cells, species *x* retains 27.3% of its total suitable habitat). By “representativeness” we refer to mean or median species' coverage by a network. Network coverage was compared between taxa, and between species in different European IUCN Red List categories (IUCN, 2015), and separately for migratory and resident bird species (BirdLife International, 2015b). Because SPA and IBA networks differ slightly in overall extent, we applied an area normalization procedure in order to compare the density (efficiency per area unit) of species coverage in separate networks (species' coverages were divided by network area (km^2), and then multiplied by 10 million to bring numbers to a more convenient scale). Statistical tests were conducted in order to explore the differences in species' coverages by SPAs and IBAs between species groupings. All GIS and statistical analyses were made with ArcGIS 10.2 (ESRI, 2015), SPSS 22 (IBM Corp, 2013) and R 3.2.2 (R Core Team, 2016).

3. Results

3.1. SPA and IBA network coverage

Currently, in the terrestrial environment, 3307 IBAs cover $634,725 \text{ km}^2$ (14.5% of the EU), while 4876 SPAs cover $543,006 \text{ km}^2$

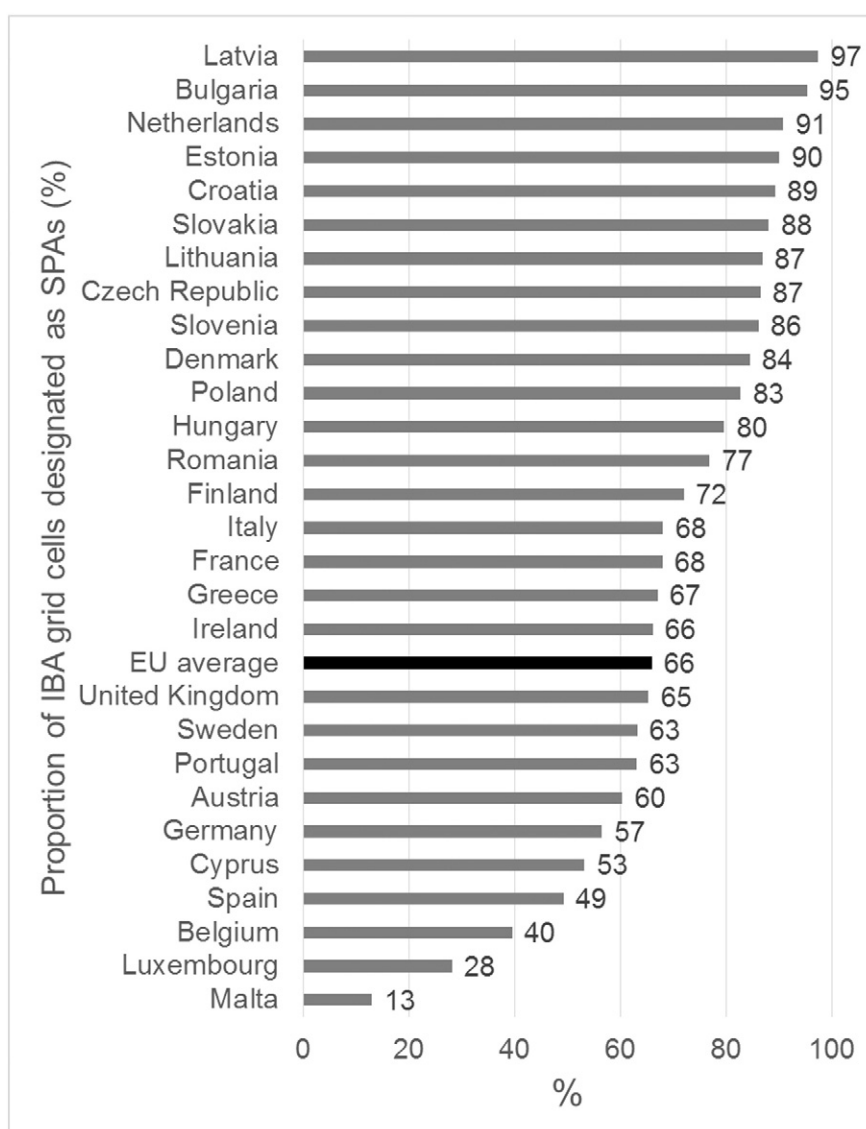


Fig. 2. Percentage of the extent of Important Bird and Biodiversity Areas (grid cells) that are designated as Special Protection Areas (SPAs) in each EU Member State (grey) and for the whole EU (black).

(12.5% of the EU). A total of 418,108 km² (9.6%) of EU land area is covered by both IBAs and SPAs (Fig. 1). Overall, 20.3% of IBAs fall almost completely (>98%) within SPAs, 55.3% of IBAs are partly within SPAs, and 24.4% of IBAs fall almost exclusively (<2%) outside SPAs. Regarding IBAs that are partly or fully covered by SPAs, on average 75.7% of the area of each IBA is covered by SPAs. In total, 66% of the IBA network area is covered by SPAs.

We found major differences in the extent of coverage and overlap between SPAs and IBAs across Member States (Table B.2). Several Member States, such as Croatia and Slovakia, have high coverage of both IBAs and SPAs (>20% of their total land area). In contrast, other Member States, such as Malta, Luxembourg and Sweden, have comparatively low coverage by SPAs (<6%, Table B.2). Coverage of land area by IBAs also varies significantly across Member States: for example, 4.3% of Sweden's terrestrial area is covered by IBAs, while 32.2% of Spain's area is covered by IBAs.

The proportion of national IBA area included within SPAs ranges from 13.0% in Malta to 97.4% in Latvia (Fig. 2). We found a positive correlation (Spearman coefficient 0.479, $p < 0.01$) between the proportion of SPA area that overlaps with IBAs and the year when the Member State joined the EU – i.e. the later that a Member State joined the EU, the higher the overlap between SPAs and IBAs.

3.2. Coverage of species distributions by SPA and IBA networks

All 837 (modeled) vertebrate species' distributions overlapped at least partially with SPA and IBA networks. We found that SPAs cover a mean of 22.9% of bird species' EU-wide ranges and 24.9% of the ranges of amphibians, reptiles, and mammals. IBAs cover a mean of 24.7% of bird species' EU-wide ranges and 27.8% for the other vertebrate species (Table B.3). Taken together, the SPA and IBA networks cover 17.3% of the EU's land area and a mean of 27.5% of the EU-wide distributions of bird species.

We compared the mean coverage of bird and vertebrate ranges by SPAs, IBAs, locations that are covered by both SPAs and IBAs, and locations that are covered only by IBAs (Fig. 3). For this comparison, we used the coverage of species distributions by each network standardized to a common unit of land (km²). Coverage density of both birds and all other vertebrates differed significantly between locations covered only by IBAs when compared to other locations (Fig. 3; $p < 0.05$, Kruskal-Wallis One way ANOVA).

There were major differences between taxonomic groups in their coverage by the SPA and IBA networks. Coverage was highest for reptiles, with a mean of 34.5% of species' EU-wide ranges covered by IBAs and 30.9% covered by SPAs, followed by amphibians (28.4% and 24.9%,

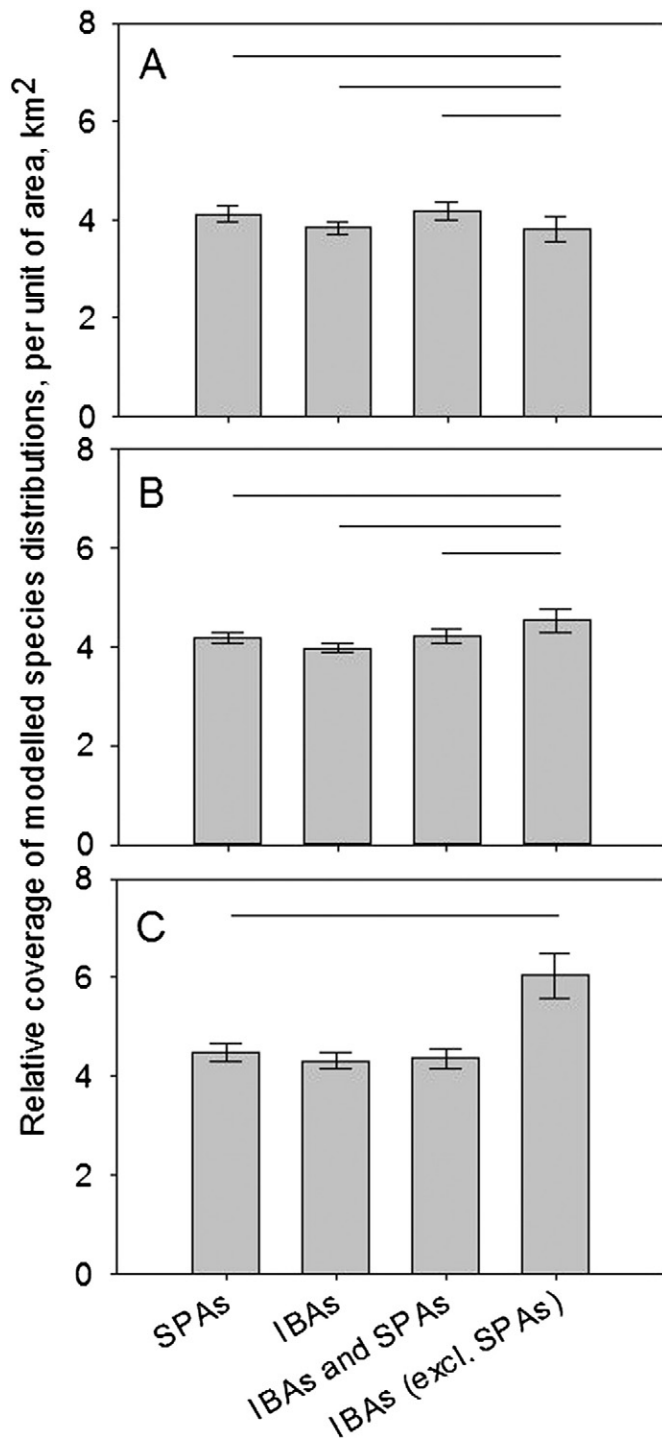


Fig. 3. Relative coverage (per unit of area) of the modelled distributions of birds (panel A), vertebrates including birds (panel B), and vertebrates excluding birds (panel C) within (1) all Special Protection Areas (SPAs), 2) all Important Bird and Biodiversity Areas (IBAs), 3) areas covered by both SPAs and IBAs, and 4) areas covered by IBAs but not SPAs. Since these networks have different total extents in the EU, coverages were standardized per unit area (km²). Error bars show standard errors of the means. Significant (pair-wise) differences (at the $p < 0.05$ level) are shown as black lines above the bars.

respectively), and mammals (22.5% and 20.3%; Table B.3). These differences were also statistically significant (Kruskal-Wallis test, $p < 0.01$).

The SPA and IBA networks provided greater coverage for the distributions of threatened vertebrate species (i.e. Critically Endangered, Endangered and Vulnerable species ($n = 110$) pooled together against Near Threatened, Least Concern, Data Deficient and Not Assessed

species ($n = 727$) based on the IUCN European assessment, Mann-Whitney U test: $p < 0.01$, Fig. 4), with 38.0% of their EU-wide ranges covered on average by SPAs compared to 41.8% by IBAs. Species listed on Annex I of the Birds Directive had on average higher coverage by SPAs (28.1%) and IBAs (30.6%) than other species (SPAs 19.2%, IBAs 20.6%), and these differences were statistically significant (Mann-Whitney U test: $p < 0.01$). Migratory bird species ($n = 343$) did not differ significantly from resident bird species ($n = 92$) in the coverage of their distributions (Mann-Whitney U test, $p < 0.853$ for IBAs and $p < 0.176$ for SPAs).

3.3. Locations that maximize species representation, and their overlap with SPAs and IBAs

The locations that maximize EU-wide vertebrate species representation are biased towards the southern Member States, with notable exceptions (Fig. 5). For example, Spain with 17.1% coverage and Finland with 11.8% coverage are among the best areas for maximizing bird species representation (Fig. 5). Somewhat in contrast, the best areas for maximizing vertebrate species representation are in Spain, Italy and Greece with a joint coverage of 44% of top areas (Fig. 5, Table B.2). Of the areas best for maximizing bird species representation, 28.2% overlap with SPAs and 27.4% with IBAs. Areas covered by both SPAs and IBAs also included the highest density of top 10% areas for birds (Fig. B.1), further highlighting the importance of these sites.

Increasing the current SPA extent from 12.5% to 17% of the EU to maximize species representation could increase the mean coverage of species distributions to 40.4% for bird species and 42.8% of all vertebrate distributions (compared with current 22.9% and 24.9%, respectively). These expansion areas are located in all Member States, apart from Luxembourg, but there were major differences between countries (Table B.4). As expected from species richness patterns, most of the optimum areas to maximize species representation for birds by expanding the SPA network are in southern and northern Europe (Fig. 6): 17.6% in Spain, 14.2% in Finland and 10.1% in Greece, although 9.6% also fall in the UK (Table B.4). Nevertheless, looking at coverage in relation to country area, some small Member States, such as Malta and Cyprus, would have over 25% of their land area covered by SPAs under this expansion scenario (Table B.4). We found that on average 9.6% of the cells for expanding SPA coverage to maximize bird species representation fall within existing IBAs. There were significant differences in this proportion between Member States: for example, 40.2% of such cells overlapped with IBAs in Spain (see Fig. 6).

4. Discussion

Important Bird and Biodiversity Areas (IBAs) are defined as the most significant locations for birds worldwide, and those in the EU were explicitly identified to serve as a blueprint for SPA designation (Heath and Evans, 2000). We show that IBAs are generally well covered by the EU's terrestrial SPA network, with three-quarters of IBAs completely or partially covered, and 66% of the total IBA network extent is covered by SPAs. However, 24.4% of IBAs have no coverage by SPAs (Table B.2). The fact that, across countries, the coverage of IBAs by SPAs correlates with the year of accession to the EU suggests that the designation of SPA networks has been significantly informed by national IBA inventories, especially since the millennium, and supports prior ad hoc evidence that this might be the case (BirdLife International, 2014).

Both IBAs and SPAs were originally identified with a focus on particular bird species of conservation concern. Here, we quantified the representativeness of terrestrial SPAs and IBAs in terms of the coverage they provide to the distributions of a larger subset of birds and other vertebrates (Appendix A). SPAs cover a relatively high mean proportion of bird distributions (22.9%) and the distributions of amphibians, reptiles and mammals combined (24.9%) within the EU. For IBAs, these numbers are marginally higher. Locations that are both IBAs and SPAs provide

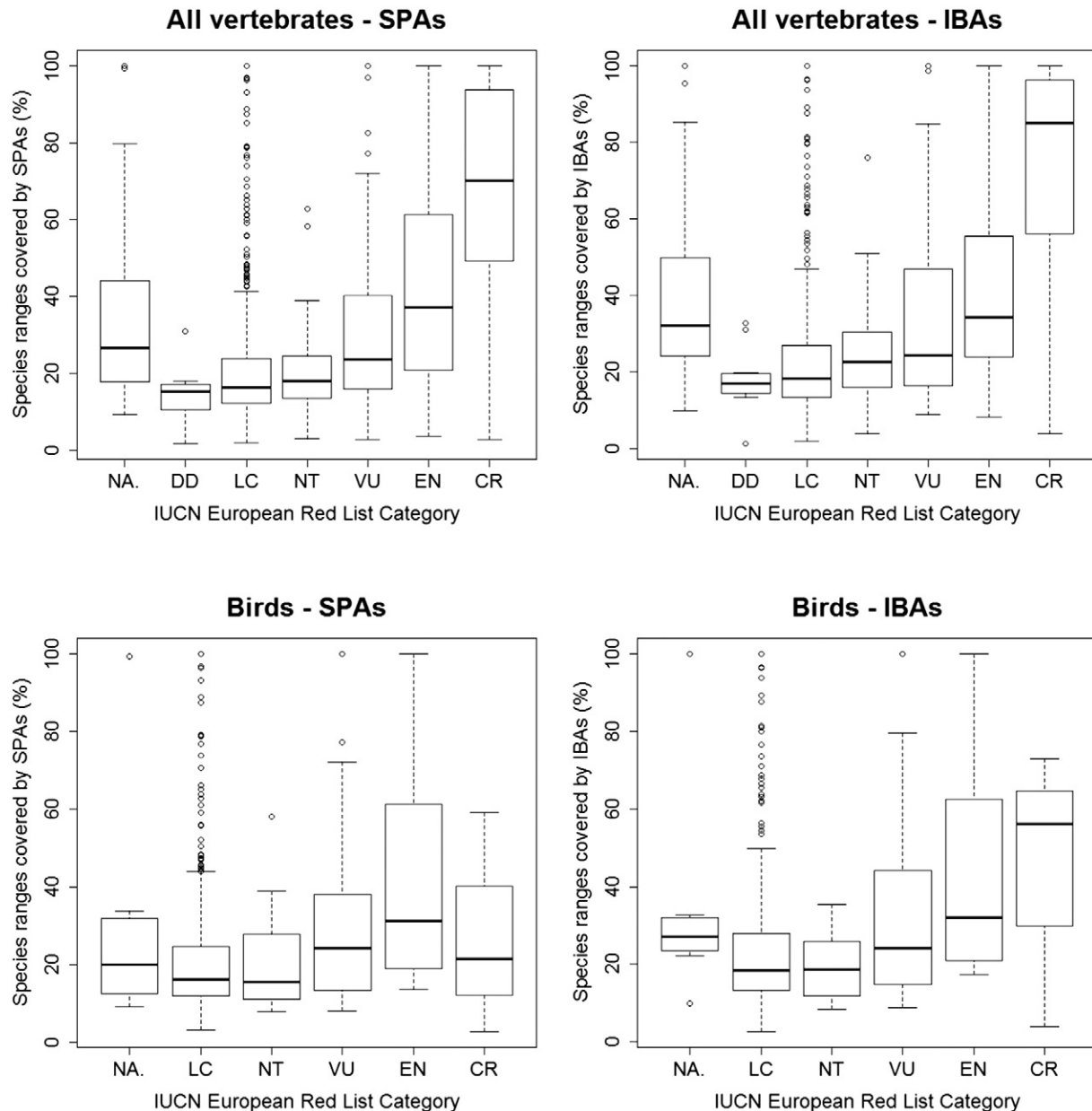


Fig. 4. Percentage of the distributions of birds and all vertebrate species (amphibians, birds, mammals and reptiles) in different European IUCN Red List categories covered by IBAs and SPAs. Medians are shown as black lines, and lower and upper quartiles are shown with the boxes and whiskers indicate 99% coverage of data. Potential outliers are shown as circles. Abbreviations for IUCN Red List categories: NA = Not Assessed, DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered.

relatively high amphibian, reptile and mammal species coverage per unit of land, and also coincide well with the areas that maximize bird species representation in the EU (Fig. 3, Fig. B.1). For IBAs, these findings indicate that, at least within a EU context, the renaming of “Important Bird Areas” as “Important Bird and Biodiversity Areas” (which was decided by BirdLife’s Global Council in 2013 to emphasize their broader significance) appears to be justified. Similar results have been reported by global studies indicating that IBAs cover large proportions of the distributions of a broad range of non-avian taxa (Butchart et al., 2012, 2015; Di Marco et al., 2015).

We found that distributions of threatened species are slightly better covered by SPAs than non-threatened species (Fig. 4). However, this could be partially explained by many threatened species having small ranges which may be more likely to be covered well by the SPA network compared with broad-ranging species. In practice, protected areas are typically the most effective conservation mechanism for range-

restricted species or those, such as many migratory waterbirds, that congregate in specific sites (Watson et al., 2014). On the other hand, many broad-ranging species, such as many migratory landbirds, are typically best conserved through landscape-scale policy mechanisms, rather than site-specific conservation approaches (Boyd et al., 2008). We found no significant difference in the coverage of the distributions of migratory and resident birds in SPAs or IBAs, possibly because the majority of European birds are migrants, and because (under Article 4.2 of the Birds Directive) migratory birds should receive the same level of protection by SPAs as those species on Annex I. However, our study was restricted to the EU; previous global studies suggest that migrants are poorly protected (Rayner et al., 2014; Runge et al., 2015), and European migratory birds may be less well protected outside Europe (e.g. in Africa).

While assessing the representativeness of protected areas, it is relevant to evaluate whether there are areas of high importance not

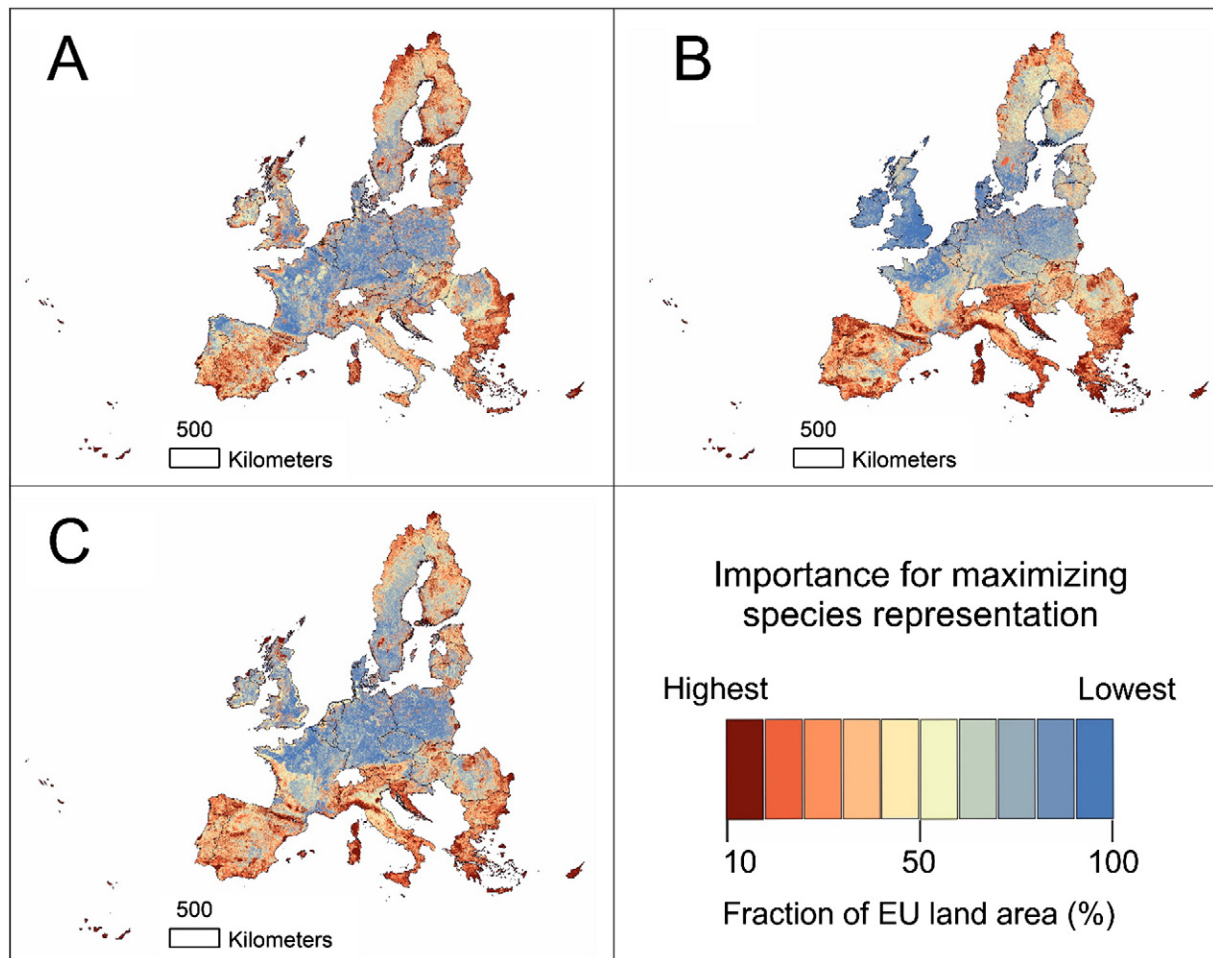


Fig. 5. Maps showing the importance of cells for maximizing representation of the distributions of birds (panel A), amphibians, reptiles and mammals (panel B), and all vertebrates (panel C) in the EU. Colours from dark red (high) to dark blue (low) show decile classes of the priority ranking from Zonation.

included in the existing network. We found that there may be good opportunities for efficiently increasing the coverage of vertebrate distributions with a relatively small expansion of the SPA network. For example, adding 4.5% of the EU land area to the SPA network (to meet the 17% of Aichi Target 11) would almost double bird species representation from 22.9% to 40.4% within this network. Such potential areas are primarily concentrated in the southern parts of the EU and near its eastern and northern borders (Figs. 5–6, Table B.4), and 9.6% of these currently unprotected locations are identified as IBAs (Table B.4). The distribution of such areas of high opportunity is non-randomly distributed among the EU states, which implies challenges in implementation and a need for cross-boundary cooperation (Dallimer and Strange, 2015). Although the likelihood of many new terrestrial SPAs being designated may be low, it is useful to know the extent and locations of gaps in the current network. Other effective area-based conservation approaches, as referred to in Aichi Target 11, may be important to ensure effective conservation of species in complex socio-ecological landscapes (Butchart et al., 2015; Santangeli et al., 2016).

The overall effectiveness of SPAs and IBAs cannot be evaluated solely based on contextual analysis like ours, using modeled species distributions and spatial prioritization tools. Obviously, other measures should also be considered for a thorough evaluation of these networks, including assessments of species' persistence and population viability, and analysis of spatial and temporal dynamics of the networks (Donald et al., 2007). In addition to all components of biodiversity, protected areas should aim to preserve the ecological processes that generate

and maintain it and provide ecosystem services. Here, we did not include ecosystem services or taxa other than vertebrates.

Our analyses that identified areas of maximum species representation assume that all species count equally (although Zonation automatically employs range-size normalization, which gives greater importance to range-restricted species in prioritization). Most species distributions can be influenced by commission errors, meaning that a distribution map indicates that a species occurs where it in reality is absent. For example, it might have been extirpated through hunting or the negative impacts of invasive alien species (Guisan and Thuiller, 2005). This issue may be of limited importance in our analyses, as the top areas identified by Zonation tend to be identified by many features simultaneously, making errors in individual maps relatively insignificant (Pouzols et al., 2014). Moreover, such commission errors could only influence our priority rankings if the areas affected are non-randomly distributed across species and space. If they are randomly distributed, then the ranking should be stable, due to the large number of species and spatial units. Nevertheless, it is always important to keep in mind the taxonomic coverage, amount, quality and limitations of the original data when interpreting the outcomes of spatial prioritization analyses.

Policy mechanisms such as the CBD and the Birds Directive guide the implementation of biodiversity conservation and on-the-ground site protection. Despite some limitations, our results add to the accumulating evidence that well-designed, scientifically-based protected area networks (such as SPAs informed by IBAs) can provide good coverage of species' distributions, including taxa that were not the original focus

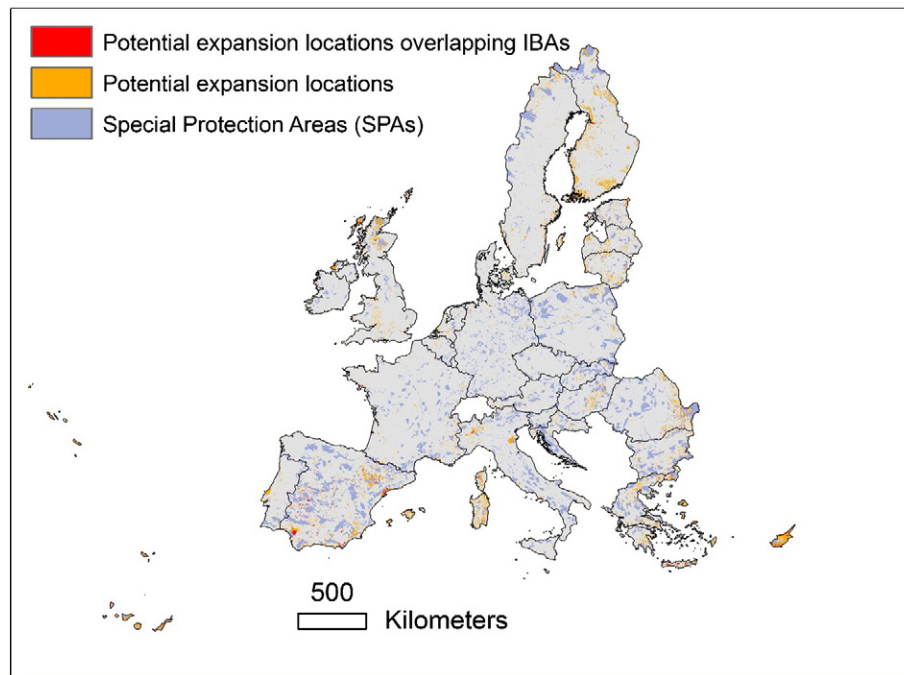


Fig. 6. Potential high-priority expansion locations for Special Protection Area (SPAs) to increase coverage from 12.5% to 17% of the EU terrestrial area while maximizing bird species representation. The locations providing highest gains for coverage of bird distributions are shown in yellow. Expansion locations that overlap with IBAs are shown in red.

of designation. We also show that small additions to the SPA network could generate substantial increases in species coverage, if site selection has a rigorous scientific basis.

Additional supporting information may be found in the online version, at <http://dx.doi.org/10.1016/j.biocon.2016.08.010>.

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