**Comparing spatial prioritization methods for biodiversity conservation and ecosystem service supply in Europe**

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**Abstract:**

Spatial identification of areas important both for biodiversity and the supply of ecosystem services (ESs) is an important part of operational decision-support for planning land-use and conservation management actions. Multiple methodological frameworks, such as multi-criteria decision making and spatial conservation prioritization, exist, but the degree to which they are applicable to both biodiversity conservation and ES still needs to be established. We compare three methods widely used in spatial conservation prioritization (rarity-weighted richness, zonation and integer linear programming) to assess their suitability for spatial prioritization integrating both biodiversity and ESs. With each method, we run a spatial prioritization analysis for 763 European tetrapod species and for 9 ESs separately. We then characterize the spatial similarity and performance of 1) the methods used and 2) for biodiversity and ESs respectively. We show that while all methods produce similar results in terms of average performance, the spatial pattern of especially the high priority ranked locations varies a great deal. Priority rank patterns for biodiversity and ESs are almost complements to each other. While the performance of the three methods is very similar, the top-fraction of solutions overlap spatially only moderately. These differences are attributed to underlying assumptions and conceptualizations in the methods. When selecting a method for spatial prioritization of both biodiversity and ESs, it is important to consider the objectives of prioritization and what the data used is actually representing.

# 1. Introduction

Land-use planning decisions increasingly need to account for both biodiversity and ecosystem services (ESs) {Formatting Citation}(Cimon-Morin et al., 2013; Cordingley et al., 2016; Goldman and Tallis, 2009; Larigauderie et al., 2012; Reyers et al., 2012)(Goldman and Tallis 2009; Larigauderie et al. 2012; Reyers et al. 2012; Cimon-Morin et al. 2013; Cordingley et al. 2016)(Schröter et al., 2016). Spatially explicit mapping of both biodiversity (Ferrier and Drielsma 2010; Maiorano et al. 2013; Meyer et al. 2015) and ESs (Mace et al. 2012; Manhães et al. 2016) and the complex interactions between the two have been intensely studied (Lavorel et al. 2017). While better models and data are still needed, more emphasis also needs to be placed on translating the knowledge learned into decision-support. There is an urgent need for spatial prioritization methods accounting both for species occurrence and the supply and demand of ESs (Luck et al. 2012; Verhagen et al. 2016). Despite the strong uptake of ESs especially in the policy-sphere (Millennium Ecosystem Assessment 2005; Demissew et al. 2015; Silvertown 2015), the operationalization of ESs into practical land-use planning is still remarkably varied across countries (Schröter et al. 2016; Prip 2017). This is most likely due to the conceptual ambiguity of ESs and the lack of clear technical articulation of what methods need to account for when working with ESs.

Spatial planning methods for ESs and biodiversity often fall into one of two broad frameworks: Multi-criteria decision making (MCDA) and spatial conservation prioritization (SCP). Whereas the former has been gaining popularity in the ES literature (Langemeyer et al. 2016; Saarikoski et al. 2016), the latter is commonly used in biodiversity conservation research (Moilanen et al. 2009). With the proliferation of available decision-support methods within both frameworks, it is worth considering what the strengths and weaknesses these methods are including the built-in, and often implicit, assumptions underlying the methods. Providing decision-support using models and computational tools is complicated and fraught with potential problems related to technical (Langford et al. 2011; Verburg et al. 2015), social (Voinov and Bousquet 2010; Hämäläinen 2015) and policy (van Voorn et al. 2016) aspects of decision-making. Only through being open and explicit about the underlying assumption, can we start to alleviate such problems.

First studies combining biodiversity and ESs in the same spatial planning framework were done already more than ten years ago (e.g. Chan et al. 2006; Egoh et al. 2007), but to date studies have mostly concentrated on one or the other. The conceptualization of the planning problem has also been mixed: sometimes biodiversity features are treated as one component of ESs (Chan et al. 2011; Schröter et al. 2014b), sometime as a separate group of features (Durán et al. 2014; Di Minin et al. 2017). Regardless of how ESs and biodiversity are conceptualized in the model, the (spatial) planning problems generally involve multiple objectives: species should be protected where they are and ES supply should be maximized where there is demand. MCDA is a branch of decision analysis dedicated for establishing best course of action given such multiple criteria and a set of potential alternatives (Keisler and Linkov 2014). It covers a broad range of methods, some of which are also spatially explicit (Mustajoki and Marttunen 2017). MCDA has been used extensively in studies addressing environmental decision-making (Zucca et al. 2008; Koschke et al. 2012; Grêt-Regamey et al. 2016; Langemeyer et al. 2016). Further, it may be particularly well-suited for the valuation of ESs because the methods can be used to analyze the performance of different alternatives (i.e. actions) in terms of evaluation criteria which in turn can include the subjective preferences of decision-makers (Saarikoski et al. 2016).

SCP can be seen as the technical, biogeographic-economic assessment of which areas are important for biodiversity and when and how actions should be implemented to achieve conservation goals (Wilson et al. 2007; Ferrier and Wintle 2009; Kukkala and Moilanen 2012)(Ferrier and Wintle, 2009; Kukkala and Moilanen, 2012; Wilson et al., 2007). In addition to ecological effectiveness, socio-economic efficiency is a key aspect of SCP: how should limited resources be invested to maximize expected outcomes (Evans et al. 2015)(Evans et al., 2015). Using simple value aggregation may be appropriate for particular ecosystem services, but less so for biodiversity (Wilson et al. 2009). While SCP was born out of need for designing effective protected area networks for biodiversity, the underlying principles and methods have been applied to many different decision-making problems, such as natural resource extraction (Kareksela et al. 2013)(Kareksela et al., 2013), habitat restoration (Thomson et al. 2009)(Thomson et al., 2009) and food production (Dobrovolski et al. 2014)(Dobrovolski et al., 2014). Especially, there are now a wide range of applications in the realm of ecosystem services (refs).

Most MCDA methods use relatively simple linear additive scoring models to combine the distinct features, even if mathematically more complex models of value aggregation are available (Keisler and Linkov 2014). The simplest way of calculating the aggregate value of, and ultimately the priority, of a given location is simply to give that location score based on features that occur there. This scoring can be done in additively by e.g. summing up the number of features (richness score) (Williams et al. 1996; Ferrier and Wintle 2009)(Ferrier and Wintle, 2009; Williams et al., 1996). In contrast, most modern methods for SCP are built with the special characteristics of biodiversity in mind. More specifically, they combine two aspects of biodiversity occurrence: rarity and richness. With this combination, we express preference for having more features over having fewer features, and having rarer features over having more common features (Arponen et al. 2005). Another central concept of SCP is complementarity, i.e. the degree to which individual sites complement the representational composition of a set of locations (e.g. protected areas). Lack of complementarity can lead to highly inefficient solutions and hence most modern spatial prioritization methods incorporate complementarity (Wilson et al. 2009; Cimon-Morin et al. 2016).

Simple scoring as value-aggregation method thus is common in MCDA and sometimes also in SCP. However, just counting the occurrence of features does not account how relatively common or rare any give feature is. A richness score adjusted by the rarity of each feature is called rarity-weighted richness (RWR) score (Williams et al. 1996; Albuquerque and Beier 2015)(Albuquerque and Beier, 2015; Williams et al., 1996). This method has the advantage of being very simple and intuitive. In addition, for simple prioritization problems RWR performs reasonably well when compared against more complex methods (Albuquerque and Beier 2015)(Albuquerque and Beier, 2015). However, this measure does not account for complementarity and hence can lead to inefficient solutions. Prioritization problems may also be solvable exactly using spatial optimization techniques such as integer linear programming (ILP) (Beyer et al. 2016)(Beyer et al., 2016). The advantage of exact optimization methods is that they produce a truly optimal solution, or if one cannot be found, a quantitative estimate on the sub-optimality of the solution reached. Additionally, more complex problem formulations, such as spatial configurations, can be accommodated. The downside, especially for more complex and realistic problem formulations, is that a complex optimization problem is quickly rendered computationally infeasible (Beyer et al. 2016)(Beyer et al., 2016), or it requires simplifications reducing the relevance of the solution (Moilanen 2008)(Moilanen, 2008). Heuristic methods strike a balance between the very simple and exact optimization methods: they are flexible enough to accommodate factors relevant for decision-making while retaining computational tractability (Moilanen and Ball 2009)(Moilanen and Ball, 2009). Two heuristic methods in particular, Zonation (Moilanen et al. 2014) and Marxan (Ball et al. 2009), are widely used both in academic research and practical planning. Heuristic methods cannot, however, guarantee the optimality of the solution and are typically on the same level of technical complexity as exact optimization methods.

Spatial prioritization of ESs is fundamentally different to that of biodiversity (Luck et al. 2012; Kukkala and Moilanen 2016; Verhagen et al. 2016). However, there are enough similarities for SCP methods to be relevant for spatial planning involving ESs. The basic problem elements are the same for spatial prioritization of both biodiversity conservation and ESs supply: quantitative and spatial features that need to be protected or secured, potential threats to the features, potential actions for retaining the features and mitigating threats, and information on the costs of potential actions (Ferrier and Wintle 2009; Luck et al. 2012)(Ferrier and Wintle, 2009; Luck et al., 2012). However, Luck et al. (2012) identified the following additional factors affecting the spatial prioritization of ESs supply: the availability of alternative means of providing benefits supplied by a given service, the capacity of ESs to meet human demand, and the site and scale dependency related to the delivery of services. Nevertheless, a simple prioritization accounting only the capacity of ecosystems to provide ES can be useful to summarize the distributional patterns of ESs (Kukkala and Moilanen 2016)(Kukkala and Moilanen, 2016). SCP methods have also been applied to prioritizing areas suitable for the supply of ecosystem services (Chan et al. 2006; Schröter et al. 2014b)(Chan et al., 2006; Schröter et al., 2014b), supply of ecosystem services and urban development (Casalegno et al. 2014)(Casalegno et al., 2014) and both supply of ecosystem services and biodiversity conservation (Moilanen et al. 2011; Reyers et al. 2012; Nin et al. 2016)(Moilanen et al., 2011; Nin et al., 2016; Reyers et al., 2012). Most studies have concentrated on single or a relatively low number of ESs features (Kukkala and Moilanen 2016)(Kukkala and Moilanen, 2016) and the suitability of the methods for ESs in particular has not been studied extensively. This is surprising given that each method to calculate spatial priorities implements a particular model of what exactly we value in the occurrence of the feature (e.g. how common or rare the feature is), how value is aggregated over multiple features, and how can we express our preferences relative to desired outcomes (**Fig. 1**).

[Figure 1 approximately here]

In this study, we have two broad objectives. First, we compare three spatial prioritization methods: rarity-weighted richness, Zonation (heuristic), and ILP approach (exact optimization) in terms of the identified priority areas for biodiversity and ecosystem services. We selected these methods because they are all built on the same conceptual foundations of combing feature richness and rarity. They differ most notably in the way each method aggregates value over multiple features(**Fig. 1**). We apply each of the methods on a prioritization problem constituting of 9 ecosystem services and the occurrence of 759 tetrapods (amphibians, birds, mammal and reptiles) on European scale. The second objective is to analyze how the assumptions underlying each method might affect the usability of the method in spatial prioritization integrating biodiversity conservation and ESs supply. This work contributes to the understanding of operational requirements of spatial planning integrating ecosystem services and biodiversity conservation, as well as developing operational instruments for such planning.

# 2. Methods

## 2.1 Area of interest

Our original aim was to cover all 28 member states of the European Union in 2017, but we had to leave Croatia, Cyprus and Malta out because they were not covered by all the selected ecosystem services and biodiversity datasets. As a result, our area of interest is a subset of EU member states of 25 countries (EU25 from now on) (**Fig. 2**). Despite of being heterogeneous both socioeconomically and biogeographically, the EU forms a coherent supranational administrative region dealing with complex environmental management structures and issues. While our aim here is not to inform any particular policy process, comparing the prioritization methods at the EU-level does at least in principle hold potential to actual policy-relevance.

[Figure 2 approximately here]

## 2.2 Data

We reviewed (non-systematically) a group of studies that have generated quantitative mappings of a broad set of ecosystem services and biodiversity in Europe and used the outputs of these studies as inputs for our prioritization analyses. We used the following criteria for selecting the datasets: 1) relevance as collection (datasets are broad and representative sample of both ecosystem services and biodiversity), 2) spatiotemporal resolution (datasets have fine enough spatial grain and are collected around the same time) and 3) geographical coverage (datasets cover the same geographical region). Screening the available datasets left us with 770 selected datasets 11 features of ecosystem services capacity (from here called data group ES) and 759 features of biodiversity features (data group BD) (Table 1).

[Table 1 approximately here]

### 2.2.1 Ecosystem services features (ES)

We selected a collection of datasets that broadly indicate supporting, provisioning, regulating and cultural ecosystem services (Millennium Ecosystem Assessment 2005)(Millennium Ecosystem Assessment, 2005). For all the ecosystem services datasets (data group ES) included, we assume a linear relationship between the estimated quantity and the perceived benefit. While some ES datasets include aspects of both supply and demand, we consider the datasets to indicate the ES capacity at any given location. The ES datasets are a subset of datasets previously collated and harmonized as part of a Horizon 2020 project PROVIDE (http://www.provide-project.eu/) and we obtained the datasets directly from project partners (Komossa et al. 2016)(Komossa et al., 2016).

For our prioritization analysis, we settled for a spatial resolution of 1 km2. This resolution is fine enough to be relevant for regional scale decision-making while still being computationally feasible at European scale. To further harmonize all the ES datasets into the same geographical extent and coordinate reference system (ETRS89 / ETRS-LAEA, EPSG:3035), we developed pre-processing components as part of the study workflow implementation (see section 2.5) using the Python bindings to the Geospatial Data Abstraction Library (version 2.0.2, GDAL Development Team 2016)(version 2.0.2, GDAL Development Team, 2016). If a dataset contained negative values (only one datasets: climate regulation), the dataset was rescaled so that all values were positive.

### 2.2.2 Biodiversity features (BD)

To assess the priority locations for biodiversity conservation in Europe, we considered the refined extent of occurrence (EOO) models for terrestrial vertebrates. The EOO models have been collated from several sources and refined to take into account the suitability of different land-use/land-cover classes based on the habitat preferences of different species (Maiorano et al. 2013; Thuiller et al. 2015)(Maiorano et al., 2013; Thuiller et al., 2015). We extracted a subset (BD from now on) of the original data for species that, according the EOO models, occur in EU25 countries, which constituted of 759 species (64 mammal, 404 bird, 83 amphibian, and 112 reptile species). The original data has a spatial resolution of 300 meters, which we aggregated to 1 km while matching the geographical extent of the ES datasets. In the aggregated datasets, the value *rij* of each cell *i* describes the fraction of the cell that is considered, by expert evaluation, to be either primarily or marginally suitable habitat for species *j*.

### 2.2.3 Administrative unit data

For delineating and selecting the area of interest, we used the spatial version of the NUTS (Nomenclature of territorial units for statistics) classification (both level 0 and level 2) for the EU available from EUROSTAT (**REF**).

## 2.3 Prioritization methods

### 2.3.1 Rarity-weighted richness (RWR)

In implementing the RWR algorithm, we followed the description originally given by Williams et al. (1996)(1996) and later revisited by Albuquerque and Beier (2015)(2015) with small modifications. More specifically, whereas Albuquerque and Beier (2015) used species presence/absence data, we do not restrict the values of features in the prioritization (ES and BD) to binary values only. Instead, the occurrence level values as present in the datasets are retained. Thus, we define RWR score *s* for cell *i* as:

(1)

where *cij* is the value of feature *j* in cell *i, wj* is the weight for feature *j*, *cj* is the sum of all cells for feature *j* and the values are summed for the *N* features that occur in cell *i*. Because the feature-specific occurrence level normalization results in relative values, the original units do not matter and the datasets are not required to be in the same scale. After summing up the RWR score, we ranked it and rescaled it into range [0, 1] to produce the final priority rank map. We calculated the RWR scores for each of the data groups resulting in three computational variants: RWR\_ALL, RWR\_ES and RWR\_BD (**Fig. S1**). Because we used many more biodiversity than ecosystem services features (763 and 9, respectively), we also defined a weighting scheme when calculating the RWR scores for the variant RWR\_ALL. The weight *wj* for a single feature *j* in data group *g* (ES or BD) is 1/*ng* where *ng* is the number of features in that group. This way, the aggregate weights for both data groups are the same, i.e., species occurrence and ES given the same importance in defining priority areas. We implemented the RWR algorithm using Python (version 3.5, Python Development Team 2016)(version 3.5, Python Development Team, 2016) and NumPy (version 1.10.4, van der Walt et al. 2011)(version 1.10.4, van der Walt et al., 2011).

### 2.3.2 Zonation (ZON)

As the second prioritization method, we used Zonation (version 4.0, Moilanen et al. 2014)(version 4.0, Moilanen et al., 2014) spatial conservation prioritization software. Zonation works on a given set of inputs that describe the occurrence of features to be prioritized in a spatially explicit manner. Starting from the full set of features, it starts iteratively removing the least valuable cells while accounting for the initial occurrence of features and the remaining occurrence of each feature. On each iteration, the features are normalized by their remaining occurrence levels, a step very similar to the occurrence level normalization in computing the RWR scores. Zonation then calculates the marginal loss value for each cell and removes the cell with the smallest marginal loss value. Zonation has several cell removal rules available for defining how exactly the marginal loss is calculated. Here, we used the Additive Benefit Function (ABF) rule, which sums the values over all features in a given cell according to a given benefit function (Moilanen et al. 2014)(Arponen et al., 2005). Given the full set of pixels *S*, the marginal loss *δ* for cell *i* is

(2)

where *Rj()* is a benefit function quantifying the value of feature *j* in the set of remaining cells *s* and *s – I* (*s*,*i* *S*) and *wj* is the weight for feature *j*. As a feature gets rarer in the cell-removal process, it also becomes relatively more valuable. This process leads to the maintenance of a balanced representation of all features in the solution. We chose to use ABF for two reasons. First, an (utility maximizing) additive benefit function (Arponen et al. 2005; Laitila and Moilanen 2012)(Arponen et al., 2005; Laitila and Moilanen, 2012) seems suitable for calculating the aggregate value of cells in our case, because the resulting priority areas will have relatively high occurrence levels of a large number of features. For ESs, this translates into giving priority to ES bundles, and for biodiversity feature, giving priority to species richness. Second, ABF can be regarded as a generalization of a maximum coverage problem (Laitila and Moilanen 2012)(Laitila and Moilanen, 2012) and hence comparable (in its simple form) to RWR and ILP methods.

We created 3 main variants for Zonation: ZON\_ALL, ZON\_ES and ZON\_BD (**Fig. S1**). In the variant with all features included (ZON\_ALL), we balanced the prioritization between data groups ES and BD by using the same weighting scheme as with RWR. We disabled the “edge removal” feature in Zonation and used warp factor of 1000, otherwise we used the default values for all parameters controlling the actual prioritization (for full implementation, see “Workflow system” below).

### 2.3.3 Exact optimization (ILP)

We also formulate the spatial prioritization problem as a hierarchical maximum coverage problem which can solved exactly with integer linear programming. In a maximum coverage problem, we seek to find a set of cells that maximizes the overall level of representation (as measured by the occurrence level) over all features while keeping the number of selected cells below a given threshold. By hierarchical, we mean solving several maximum coverage problems using the top priority fraction of the landscape as a constraint. Before solving the optimization problem, we occurrence level normalized all features:

(3)

where *cij* is the value of feature *j* in cell *i* and *cj* is the sum of all cells for feature *j*. We define the optimization problem as:

(4)

where *xi* {0,1} indicates whether cell *i* is included in the solution or not, *rij* gives the occurrence level of feature *j* in cell *i* and *wj* is the weight given to feature *j*. As a constraint, we define that the number of cells included in the solution must be smaller than a given fraction of the landscape *c* {0.01, 0.02, …, 1.00}. We used Gurobi optimization solver (version 7.0.0, Gurobi Optimization Inc. 2016)(version 7.0.0, Gurobi Optimization Inc., 2016) and its Python bindings for solving 100 optimization problems defined above. Gurobi is a proprietary software using multiple algorithms to solve linear programming problems with a guarantee, given enough time, of finding an optimal solution or a gap measure of the level of sub-optimality.

After solving the optimization problems, we aggregated the solutions into a hierarchical priority rank maps by first calculating the selection frequency of each cell over solutions for each value of *c*, then ranking the result and rescaling it into range [0, 1]. We repeated this procedure to the 3 main variants: ILP\_ALL, ILP\_ES and ILP\_BD (**Fig. S1**). In the variant with all features included (ILP\_ALL), we balanced the prioritization between data groups ES and BD by using the same weighting scheme as with RWR in the optimization.

## 2.4 Comparing solution similarity and performance

We compared the solutions for all nine variants (**Fig. S1**) for the solution i) similarity and ii) performance. In addition, we also quantified to overall patterns in rank priorities over all solutions.

To quantify the different aspects of the similarity between the solutions, we used three different measures. First, to account for the spatial overlap we calculated the Jaccard’s index between solution subsets. Jaccard’s index *J* between solutions A and B is calculated as dividing the number of cells in both A and B by the number of cells in either or both solutions (for implementation details, see “Workflow implementation”). Value of *J* = 1 indicates a complete overlap between the solutions (or subsets). In addition to calculating *J* between the best 10% of all solution pairs, we also calculated J for the worst 10%. Second, we computed the rank correlation coefficients (Kendall τ, tau-b accounting for ties) between the priority rankings in all solutions using the implementation available in Scipy (Jones et al., 2001; Knight, 1966). Third, to quantify the similarity of the solutions when the aggregated to a meaningful administrative level (NUTS2 regions), we computed the Map Comparison statistic (MCS) between all solutions pairs. MCS is an index summarizing the relative difference between spatial datasets as the average difference between mean ranks in NUTS2 regions, expressed as a fraction of the highest value (Schulp et al. 2014)(Schulp et al., 2014):

(5)

where *a* and *b* are the mean ranks in a particular NUTS2 region and *N* is the total number of NUTS2 regions considered. To present MCS in the same scale as the Jaccard’s index and Kendall τ (1.0 signifies solutions are the same), we use *1 – MCS*.

We also examined how well the different methods performed compared to each other. As a performance measure, we use how much of the overall feature representation levels can be covered by a given fraction of the landscape. While Zonation produces this type of performance data automatically, our RWR and ILP implementations do not. We used the so-called solution loading functionality in Zonation to compute performance data for RWR and ILP. This way, the priority rank solution produced by RWR and ILP is loaded into Zonation, which then proceeds with the usual cell-removal following the rank order from the loaded solutions while also producing the performance data (Moilanen et al., 2014). We used this pre-loading functionality in two ways. First, using only ZON we examine the trade-offs in prioritizing areas on all available features (ALL) as opposed to ESs (ES) or biodiversity features (BD) only. Second, we compare the RWR and ZON solutions to the ILP solution. The Gurobi solver is the only method that produces a measure of the optimality of the result thus giving a benchmark against which the sub-optimality of the solutions produced by the other methods (RWR and ZON) can be compared to.

To quantify how similar the average rank priories calculated for each NUTS2 regions are, we also calculated the mean and the standard deviation of the priority rank of all NUTS2 regions over all solutions.

## 2.5 Testing for the effect of including costs

The spatial prioritization can be made more relevant for real-life planning by incorporating factors such as costs, ecological condition and connectivity into the methods (Ferrier and Wintle 2009). However, which factors can be accounted for by the prioritization methods varies greatly and comparing the prioritization becomes increasingly more difficult as every new layer of complexity comes with additional model assumptions. Therefore, we chose to concentrate our comparison on the simple (i.e. comparable) basic setups for each method. In addition, we also tested how an additional prioritization option, including a proxy for costs, would affect the results of each method. The following results section presents all prioritization analyses without costs, but a subset of analyses including costs can be found in the Supplementary Material.

## 2.6 Workflow implementation

We combined the individual processing steps of data pre-processing, analyses and post-processing in a semi-automated workflow using the Snakemake workflow engine (version 3.10.0, Köster and Rahmann 2012). The complete implementation is available at XXX.(Köster and Rahmann, 2012)

# 3. Results

## 3.1 Spatial patterns and similarity

The priority rank maps showed different spatial patterns when accounting for either species occurrence, ecosystem services or both. With all features included in the analyses (ALL), the highest priority areas were found mostly in Southern Europe (Spain, Italy and Greece) and South Eastern Europe (Bulgaria and Romania) with some priorities also in Northern Fennoscandia (**Fig. 3A-C**). The highest priority areas for ESs only (**Fig. 3D-F**) were concentrated in mountainous regions in Central Europe, Spain and Italy. We identified more isolated high-priority areas also in the North-Western UK and Portugal as well as in the southern part of Fennoscandia. The priority rank patterns for biodiversity features (BD) had a distinct bimodal distribution with high priority areas both in the south (the Mediterranean basin) and north (the subarctic Fennoscandia) (**Fig. 3H-I**). The patterns on rank priorities were spatially much more similar when compared across the different methods (RWR, ZON and ILP). On a visual inspection, RWR (**Fig. 3A**, **3D** and **3H**) and ILP (**Fig**. **3C**, **3F** and **3I**) produced almost identical priority patterns, whereas ZON (**Fig. 3B**, **3E** and **3G**) produced slightly more dispersed priority patterns.

[Figure 3 approximately here]

On an aggregate NUTS2-level, the mean rank priorities over all nine analysis variants were the highest in central and southern Europe (**Fig. 4A**). The only exception to this general pattern is Finland, for which the rank priorities in all variants were relatively high. Both the highest and lowest mean rank priorities were quite consistent over the different analysis variants as measured by the standard deviation of the mean rank (**Fig. 4B**) with two exceptions. First, the larger part of Southern Europe (Southern Spain, Greece, Corsica and Sardinia) had high mean rank and relatively high variation across variants. Second, Central Europe (North-Eastern France, Southern Germany) had medium high ranks and relatively high variation across the variants.

[Figure 4 approximately here]

Quantitative comparison of the priority rank using the various comparison statistics was in line with the visual observations of the similarity between the different data groups and methods. Between the data groups and within the methods, ES and BD solutions were not correlated with Kendall tau correlation coefficients of -0.04 for RWR and ILP, and -0.03 for ZON (**Fig. 5A**). Both ES and BD were moderately correlated with ALL with correlation coefficients of 0.42, 0.45 and 0.45 (ES) and 0.53, 0.51 and 0.49 (BD) for RWR, ZON and ILP. On a more regional scale, the MCS gives similar results with MCS of 0.60, 0.61 and 0.60 between ES and BD in RWR, ZON and ILP respectively (**Fig. 5B**). Compared to ALL, MCSs were 0.70, 0.69 and 0.69 for ES, and 0.80, 0.82, 0.80 for BD (RWR, ZON and ILP respectively). The spatial overlaps as measured by the Jaccard’s coefficient between the best and worst 10% of the solution were, again, similar between the data groups and within the same method. The overlaps between the best 10% of solution ranged from 0.04 (between ES and BD for all methods) to 0.52 (RWR\_BD / RWR\_ALL) (**Fig. 5C**). The worst 10% of all solutions were very similar ranging from 0.95 (ES / BD in all methods) to 0.97 (BD / ALL in all methods) (**Fig. 5D**).

Between the methods and within the data groups, solutions produced by RWR and ILP in particular were very similar. The rank correlation coefficients for the different data groups between RWR and ILP were 0.91, 0.99 and 0.99 for ALL, ES and BD respectively (**Fig. 5A**). Rank correlation between RWR and ZON (0.90, 0.93, 0.92 for ALL, ES and BD), and ILP and ZON (0.87, 0.93, 0.92 for ALL, ES and BD) were not quite as high but still very strong. MCSs were equally strong between the methods ranging from 0.92-0.97 between ZON and ILP to 0.91–0.99 between RWR and ILP (**Fig. 5B**). Between RWR and ILP, the spatial overlaps of the best 10% of the solution were 1.0 (exactly the same) for ES and BD, but only 0.51 for ALL. Between ZON and both RWR and ILP, however, overlaps were more modest (0.52, 0.64, 0.64 for ALL, ES and BD) (**Fig. 5C**). The worst 10% of the solution were almost completely overlapping (0.97-1.00) for RWR, ZON and ILP (**Fig. 5D**).

[Figure 5 approximately here]

## 3.2 Solution performance and optimality

The performance of all methods was very similar for variants RWR\_ALL, ZON\_ALL and ILP\_ALL (**Fig. 6** and **Table 2**). The median performance over all features for the best 10% of the solution (i.e. the median value of feature occurrence level covered by the best 10% of the solution) was 18.5%, 19.1% and 15.3% for RWR, ZON and ILP, respectively (**Table 2**). For some features, the top 10% fraction of the solution covered 100% of the occurrence level and so the mean performance levels were higher for all methods (34.7%, 30.6% and 25.4% for RWR, ZON, and ILP). While RWR achieved the highest mean performance, both ZON and ILP had a more balanced performance over all features as shown by the interquartile range (**Fig. 6**) and higher median value for the top 10% fraction (**Table 2**). This is particularly so for ESs, which have a higher median performance for ZON (14.5%) and ILP (12.8%) than for RWR (9.8%). Over the whole solution (**Fig. 6**), ZON achieves a more balanced solution as compared to both RWR and ILP.

[Figure 6 approximately here]

[Table 2 approximately here]

Including a proxy for the cost of conservation or management action (Supplementary Material) had an effect of making the both the spatial priority patterns and performance between the different methods more similar. [TBA] (describe where the results are to be found)

# 4. Discussion

While the origin and computational implementation of the different methods compared in this study is different, the spatial priority patterns produced by and the overall performance of the different methods were very similar. The similarities can be explained upon reconsidering the method designs and expecially our implementation of the methods. To avoid apples-and-oranges comparisons, we chose methods that are variations on the same underlying concept and harmonized the implementions as far as the methods allowed.

## 4.1 Priority rank patterns

The overall similarity between priority rank patterns produced by the different methods was very high: as measured by the correlation between priority rank rasters, RWR and ILP were practically the same for ES and BD, and ZON was very similar (**Fig. 4**). This similarity also applies to the best (worst) 10% of the solution for RWR and ILP, less for ZON and the two other methods. High overall correlation and relatively smaller overlap of the top fraction is to be expected if there is variation between methods in how the highest priorities are defined. Since spatial prioritization is often done to identify the top fraction, this is an important message to keep in mind. For ALL, however, the spatial overlap for the top 10% fraction was surprisingly low between RWR and ILP. This is most likely due to the implementation of ILP and the way in which we balance the feature groups (ES and BD) through weighting.

The priority maps produced are informative for examining the distributional patterns of both biodiversity and ES features. For ES, the highest priorities were concentrated in Central Europe (**Fig. 3D-F**). Using different set of ES features, Mouchet et al. (2017)(2017) found high diversity of relative representation of ES bundles in roughly the same regions that have high priorities in our analyses. Not only have the regions high diversity if ESs, the also have capacity for some of the rarer ESs, which is what all the methods in this study account for. Two ES features in particular had a high influence on the patterns. Erosion prevention has high values in mountainous regions, but is relatively rare elsewhere. Carbon sequestration and wood production had a minor, but still noticeable effect concentrating priorities in Southern Fennoscandia and South-Western France. For BD, the distributional pattern for all solutions was bimodal in terms of latitudinal gradient (**Fig. 3G-I**). Since all methods prioritize based on a combined measure of rarity and richness, the interpretation is that both the southern (the Mediterranean basin) and the northern (the subarctic Fennoscandia) have relatively many species with restricted range-sizes. This result is qualitatively the same as what Kukkala et al. (2016)(2016) observed for 395 terrestrial vertebrate species listed in the EU nature legislation, a subset of the data used in this study.

Since there are differences in where the priorities are especially for ES and BD variants, a simple approach in identifying areas that are consistently high priorities over all nine variants is given in **Fig. 3A**. Reflecting the priority patterns already discussed, Southern Europe is higher priority on average than Northern Europe (except for Finland, which receives medium priorities). Further analysis (**Fig. 3B**) shows how consistent the priorities are across the nine variants. For example, Central Europe and Greece both have relatively high mean rank (**Fig. 3A**), but also high relative variation in the mean rank (**Fig. 3B**). This is caused by ES variants having high priority rank in the former, and BD variants in the latter. In operative context, developing a single (or few) prioritization(s) would be a better option than averaging over several prioritizations with different objectives, but such averaging may serve as a useful first approximation.

## 4.2 Method performance

The performance of the different methods was very similar across the variants in the same feature group (**Fig. 4**), but some differences are worth noting. Overall, ZON produces a more balanced solution throughout the whole priority range (**Fig. 4C-D**). This is evident from a higher median value over all features, narrower interquartile range, and higher minimum and lower maximum values. This balance is achieved through the iterative cell removal process (Moilanen et al. 2014), which the other two methods do not have. This balance is also reflected when we consider only the top 10% fraction of the solution for ALL variants: ZON achieves a higher median performance for feature groups ES and BD (14.5% and 19.4%, respectively) than RWR (9.8% and 18.9%) or ILP (12.8% and 15.4%) (**Table 2**). Similarly, ILP retains a better balance between the two feature groups that RWR. RWR on the other hand has the highest mean performance value for the top 10% fraction (34.7%) when compared to ZON (30.6%) and ILP (25.4%). While differences in our case are small, they do emphasize an important point: if balance between multiple feature groups is desired, then ZON or ILP is a better option than RWR. In reality, this balancing effect will depend on the characteristics of the prioritization features used and the number and relative structure of the feature groups. What is also noteworthy is that depending on the prioritization features, similar performance levels can be attained with different spatial configurations. This can be observed also in our results: while the performance levels are relatively similar between all features, the best 10% fractions of the solutions overlap spatially only moderately (**Fig. 6**). Therefore, it is always a good idea to examine how the performance and the location of top priorities are related for a given prioritization method.

Our results are also in line with Albuquerqeue and Beier (2015) in(2015) that the performance (measured as mean over all features) of RWR is slightly better than Zonation for a set of plant and bird species in Africa, Europe and North America. However, where Albuquerqeue and Beier (2015) used the core-area cell-removal rule in Zonation (CAZ), we chose to use the additive benefit function rule. ABF is conceptually closer to our implementations of RWR and ILP and thus forms a better basis for comparison. Which one of ABF (somewhat emphasizes richness) or CAZ (somewhat emphasizes rarity) is better suited for prioritization of ESs in particular is an important question, but outside the scope of the current work. However, we do highlight the importance of addressing this question whenever deciding which method is used for the prioritization analysis.

## 4.3 Integrated prioritization of biodiversity conservation and ecosystem services supply

The validity of the spatial priorities we have produced rests upon whether or not the core-principles of our methods, a combination of rarity/richness and value aggregation, makes sense when we consider the spatial nature of ESs included. In terms of richness, providing multiple ESs in the same location can certainly be desirable. However, it is important to understand the conceptual and practical implications between ES capacity (the long-term potential of ecosystems to provide services under given management regimes) and ES flows (the actual use of ES), which is still different from ES demand (individual agents’ preferences for specific ESs) (Schröter et al. 2014a; Verhagen et al. 2016)(Schröter et al., 2014a). Given this interplay between capacity, flow and demand, valuing rarity of ESs is not straight forward either. For some ESs, such as recreational value, lower supply capacity (rarity) may translate into higher value. For others, such as carbon sequestration, not necessarily so (in principle, the first carbon ton sequestered is as valuable as the nth). A full spatial prioritization for ESs should therefore consider the capacity of ecosystem services to meet human demands, the scaleof, and site dependencyin, the delivery of services (flows), and the availability of alternative meansof providing benefits supplied by services (Luck et al. 2012; Verhagen et al. 2016)(Luck et al., 2012). Depending on the ESs under consideration, spatial connectivity may also be relevant (Kukkala and Moilanen 2016).

Nevertheless, the prioritization principles we have considered here are highly relevant for biodiversity and hence a prioritization scheme including biodiversity should incorporate them on some level. Spatial prioritization including only ES capacity and biodiversity serves as the first step towards a fully operational planning with emphasis on the occurrence of biotic features and their capacity to provide ESs. Biodiversity underlies all ecosystem services, but the relationship between the two is non-linear, complex and often case-specific (Reyers et al. 2012). It does not follow that priority areas for the supply of ecosystem services are automatically priority areas also for biodiversity (Anderson et al. 2009; Thomas et al. 2012). Our results show this clearly as the top-priority areas for ES and BD are almost complementary (**Fig. 3D-I**). Furthermore, much of the work done has been concentrated on analyzing the co-occurrence of biodiversity and ESs in order to identify so-called “win-win” outcomes (Wilson and Law 2016). Such framing may be appealing for policy-makers facing difficult decisions, but in reality we are more probably faced with multiple trade-offs between biodiversity and ESs (McShane et al. 2011; Cordingley et al. 2016). For example, using the C-Plan SCP software in eastern Canada, Cimon-Morin et al. (2016)(2016) reported a two to five-fold reduction in efficiency in a conservation area network built primarily either for ESs or biodiversity features as opposed to considering both simultaneously. When doing prioritization for both ESs and biodiversity features, the best strategy is to prioritize both separately and together in order to quantify the trade-offs involved (Kukkala and Moilanen 2016). The ability to identify and quantify such trade-offs is one of the main motivations for spatial prioritization and warrants further research.

## 4.4 Selecting the right tool

Our findings show that the difference between the three prioritization methods we used are relatively small and subtle, but still important when considering which method to use for spatial prioritization of both biodiversity and ESs. RWR performs well when there is no special need to emphasize balance between prioritization features or feature groups. ZON produces a more balanced solution with still high average performance. ILP is in between RWR and ZON in terms of the balance, but guarantees an optimal solution. When considering both feature groups ES and BD in the prioritization, the spatial overlap between the solution top-fractions were only moderate. This is important, because it implies that relatively similar performance can lead the different spatial locations of the top priorities. We did not quantify what exactly drives spatial location of top priorities for each method, but in future studying this topic would be useful. To facilitate such studies, we also make our workflow and method implementation free and open source for anyone to improve upon.

From technical perspective, RWR has the advantage of being very simple to implement and execute. In our case, using a cloud-based server configuration running Ubuntu 14.04.5, an Intel Xeon E5-2698 2.30GHz CPU and 70 GB of RAM, executing RWR\_ALL took approx. 10 minutes to complete, whereas ILP\_ALL took approx. 2.5 hours and ZON\_ALL approx. 2.6 days. Such comparison, however, is useful only insofar as the spatial prioritization problem is kept very simple. The main reason for ZON taking much longer to complete is the iterative cell-removal process, which can also be considered as desired feature lacking in the two other methods. Simplicity and speed are both valuable features of a method supposed to provide support for decision-making, but both come with a prize: simple and fast methods may not be able to accommodate all the components required to model a real-life spatial prioritization problem. For example, our current analysis assumes no spatial interactions within or between the features included in the analyses. In reality, however, spatial connectivity between the planning units (pixels) is probably required both for biodiversity (Lehtomäki et al. 2009; Beyer et al. 2016) and(Beyer et al., 2016; Lehtomäki et al., 2009) ESs features (Kukkala and Moilanen 2016)(Kukkala and Moilanen, 2016). Cost-effective spatial prioritization often also requires prioritizing between actions, not places (Brown et al. 2015)(Brown et al., 2015). This implies, that prioritization methods used should be capable of factoring in costs (see also Supplementary Material), condition, and clearly defined objectives and benefits (Evans et al. 2015)(Evans et al., 2015). Equally, for ESs models for capacity, flows and demand potentially need to be incorporated (Luck et al. 2012; Schröter et al. 2014a)(Luck et al., 2012; Schröter et al., 2014a). If this is the case, then simple methods such as RWR simply are not enough.

Operationalizing ESs into spatial planning and decision-support systems is not, however, only a technical issue. It also requires institutional adaptation, case-specific tailoring of methods, and deliberation among practitioners and stakeholders (Rinne and Primmer 2016). For any method to be seriously considered as decision-support tool, it must address these aspects and many more (Voinov and Bousquet 2010; Bagstad et al. 2013; Lehtomäki and Moilanen 2013; Rose et al. 2016; van Voorn et al. 2016). Operational tools must facilitate the translation of high-level objectives into something that they can analyze (low-level objectives, see **Fig. 1**) either directly, or this must be done by operators familiar with the tool. Both MCDA (e.g. Saarikoski et al. 2016) and SCP (Knight et al. 2009) frameworks include this facilitation process, and in principle, all of the methods we have used could be used within either framework.

In our opinion, the so called “model-on-the-shelf” (van Voorn et al. 2016) phenomenon is all too common in selecting decision-support methods: with severe time and resource limitations, it is often tempting to re-use existing models and methods without proper consideration of their fundamental applicability to the problem at hand. There is also a tendency to concentrate on model *outputs* (articles, software, data) rather than *outcomes* (real-world socio-ecological changes) (Matthews et al. 2010). We believe that the much needed shift in emphasis from outputs to outcomes is facilitated by careful consideration on which methods are perceived not only credible, but also salient and legitimate (van Voorn et al. 2016) by a broad community of scientists, decision-makers and stakeholders. Our work is a small, but resolute step to that direction.

# 5. Conclusions

[TBA]

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# Figure captions

**Figure 1.** Spatial prioritization methods in the broader context of environmental decision-making. In their core, all methods used in this study (RWR, ZON and ILP) construct the priority rank in a very similar way: the priority of any given location is fundamentally defined by a simple rule that more is better than less (richness) and that rarer is better than common (rarity). Differences start to emerge in the way the different methods aggregate value over multiple features. Methods are also different in how well they can accommodate other relevant factors, such complementarity. Ability to handle such factors also means increased complexity and increased demand for computational and human resources. Ultimately, which method (if any) is the most suitable depends on the overall objectives of the prioritization, and can usually be determined only through the process of translating high-level objectives into low-level objectives.

**Figure 2.** The 25 European countries included in the study.

**Figure 3.** Priority rank maps (spatial solutions) for the nine analysis variants in the study. The maps are grouped by method used (RWR, ZON and ILP) in columns, and by data groups (ALL, ES, BD) in rows. The color scale indicates rank priorities from the lowest 20% (in blue) to the highest 2% (in red).

**Figure 4.** Mean priority rank and standard deviation of mean priority ranks over all analysis variants in NUTS2-regions. Both measures are calculated over 9 different analysis variants (see Fig. 3).

**Figure 5.** Similarity between all analysis variants as measured by A) Kendall’s Tau rank correlation, B) map comparison statistic, and Jaccard’s coefficient between the best 10% (C) and the worst 10% (D) of all solutions. All statistics are symmetrical between the solutions compared, hence the lower triangular matrix is omitted.

**Figure 6.** The performance of variants RWR\_ALL, ZON\_ALL and ILP\_ALL. Each prioritization is based on both feature groups (ES and BD), but the results are shown per feature group. Solid lines show the median value of how much a given fraction of the landscape (x-axis) covers of the feature occurrence levels (y-axis) in a given feature group. The grey shaded area shows the interquartile range and is delineated by upper (75%) and lower (25%) quartiles and hence show the performance distribution of 50% of features within the group. Dashed line indicates the minimum and dot-dashed line the maximum over all features within the group. Panels show feature-group performance per spatial prioritization methods used: RWR (**A** and **B**), ZON (**C** and **D**), and ILP (**E** and **F**). The vertical dotted line and purple shading indicate the top 10% fraction of the solution.

# Figures

Figure 1.

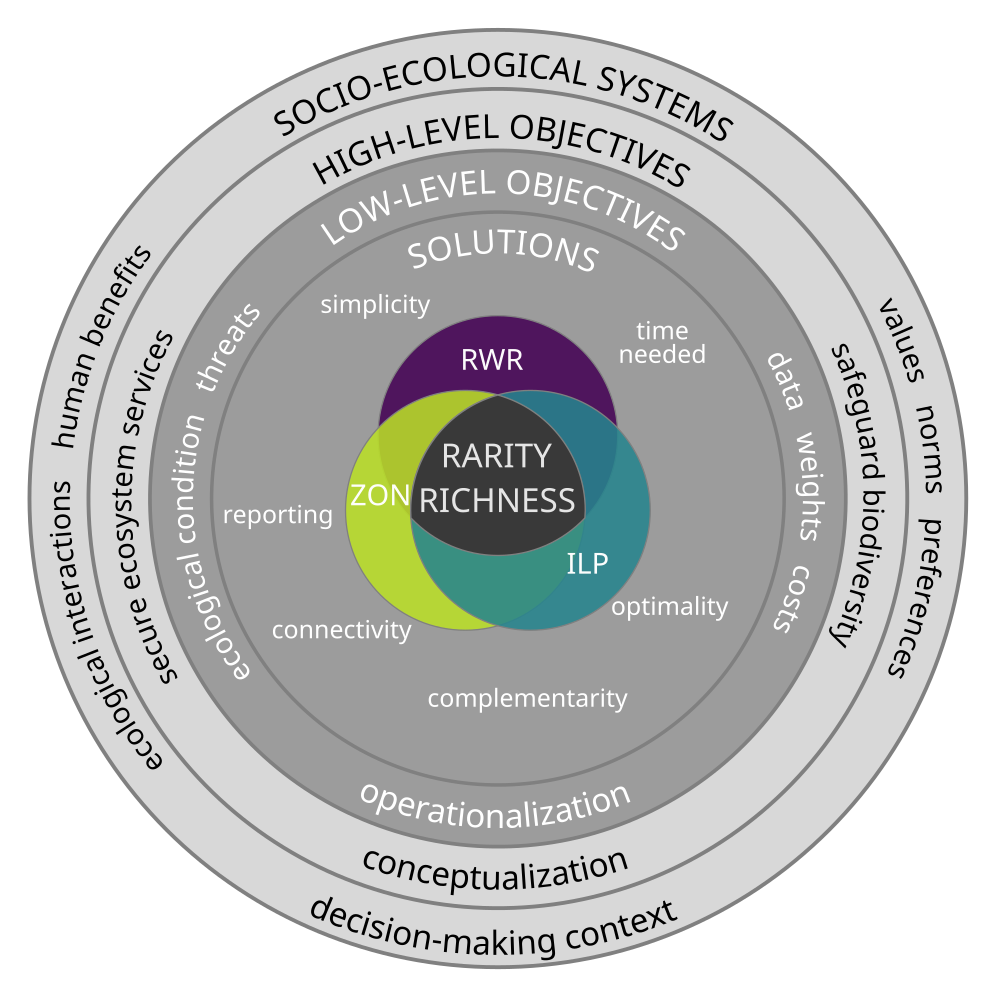


Figure 2.

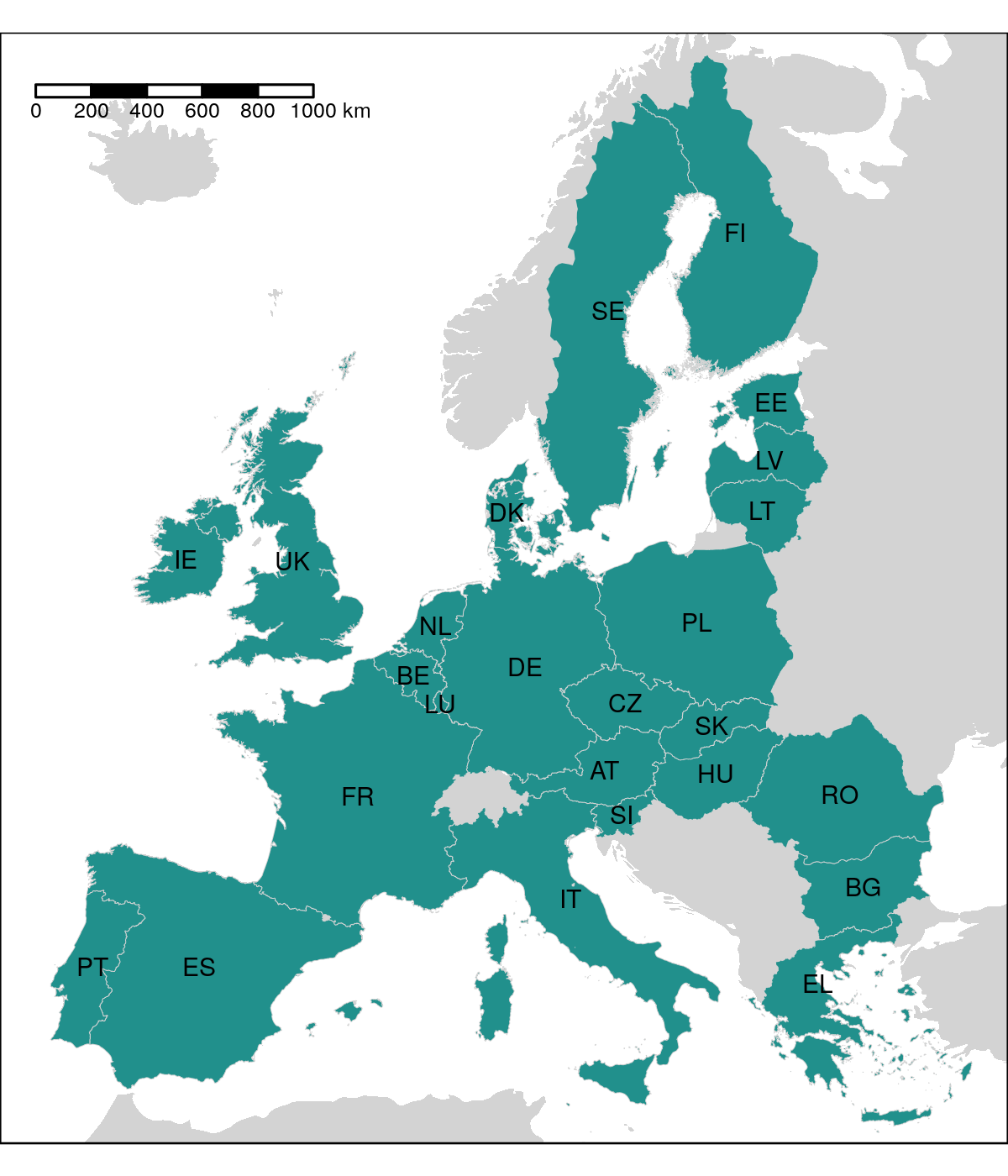


Figure 3.

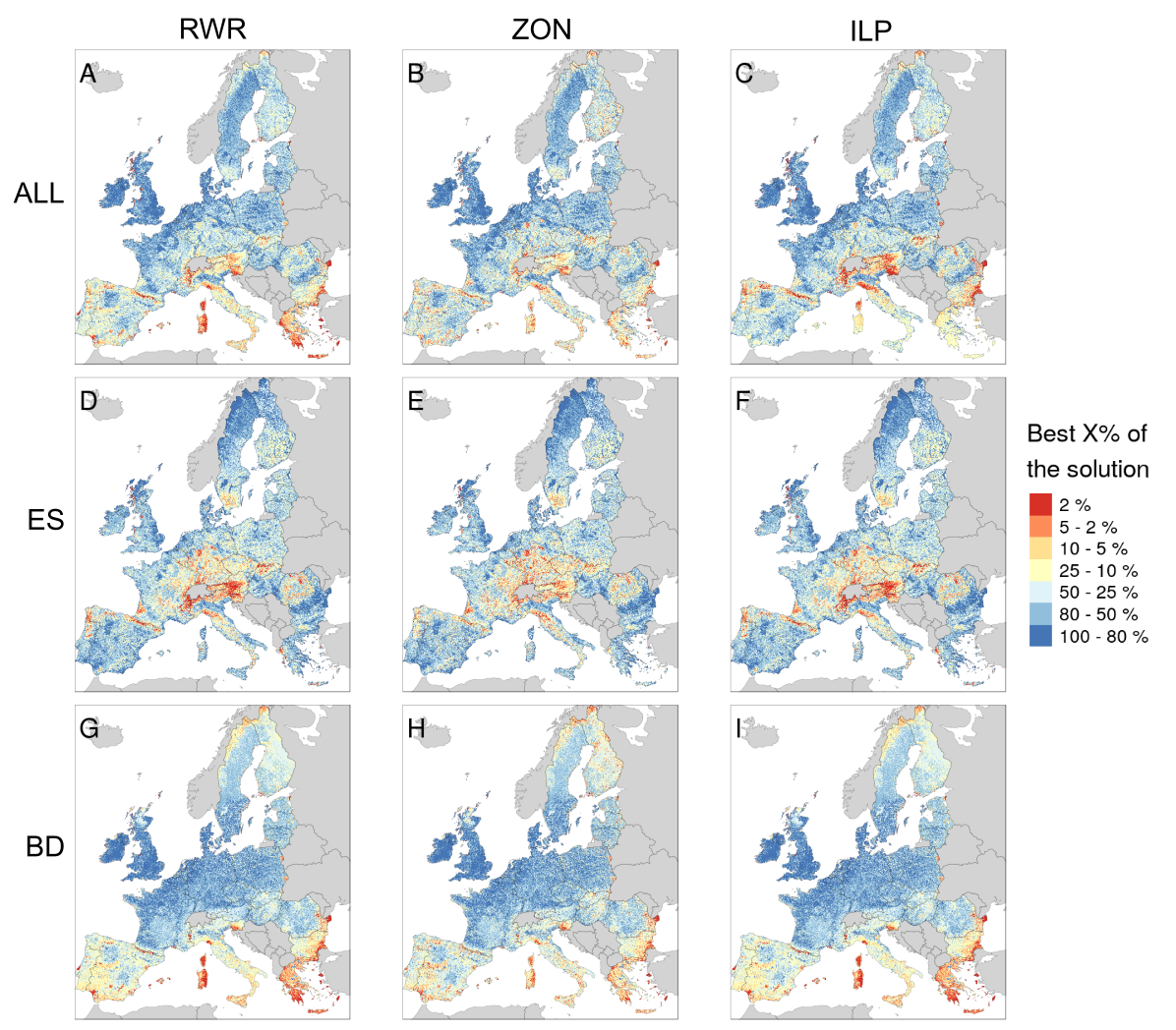


Figure 4.

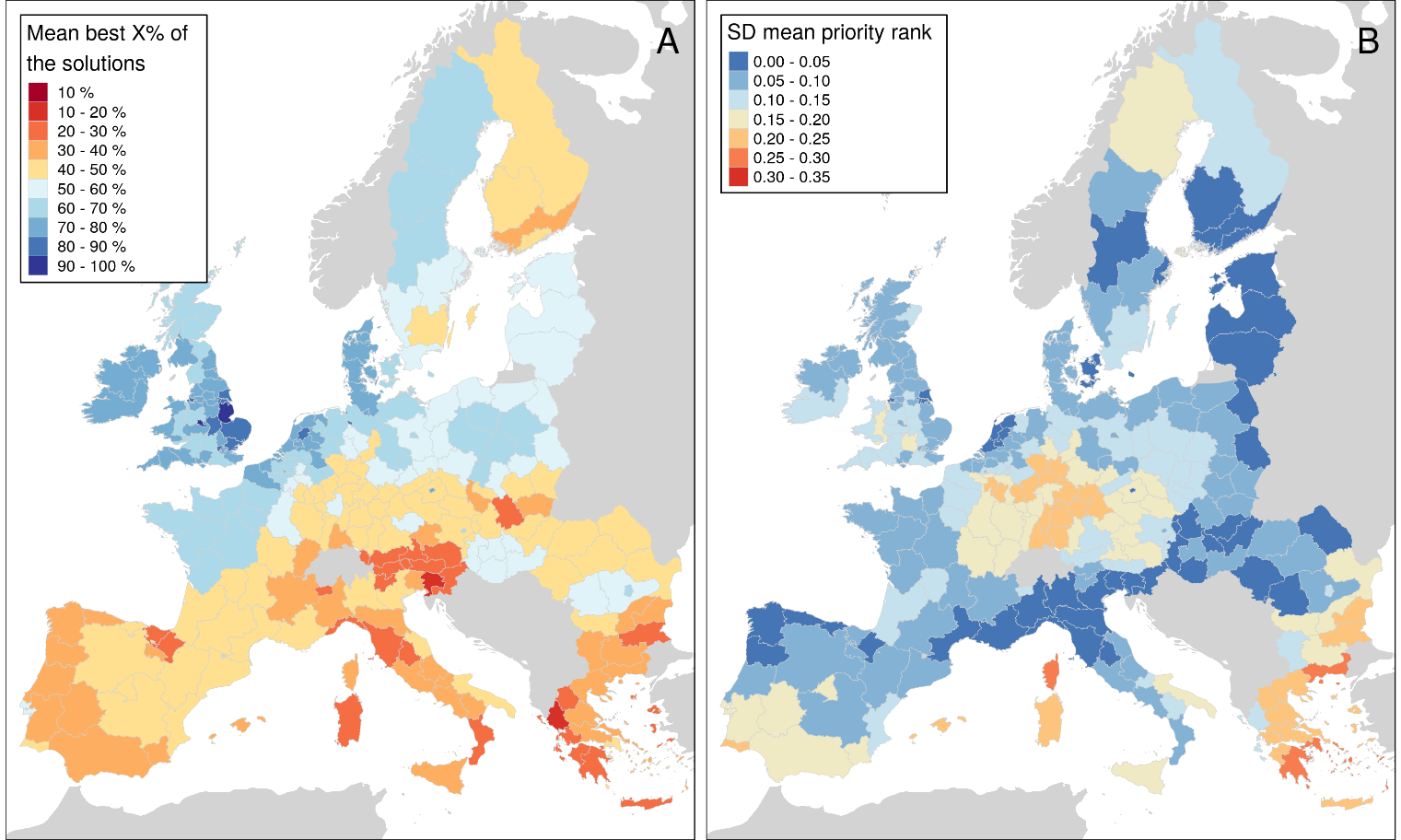


Figure 5.

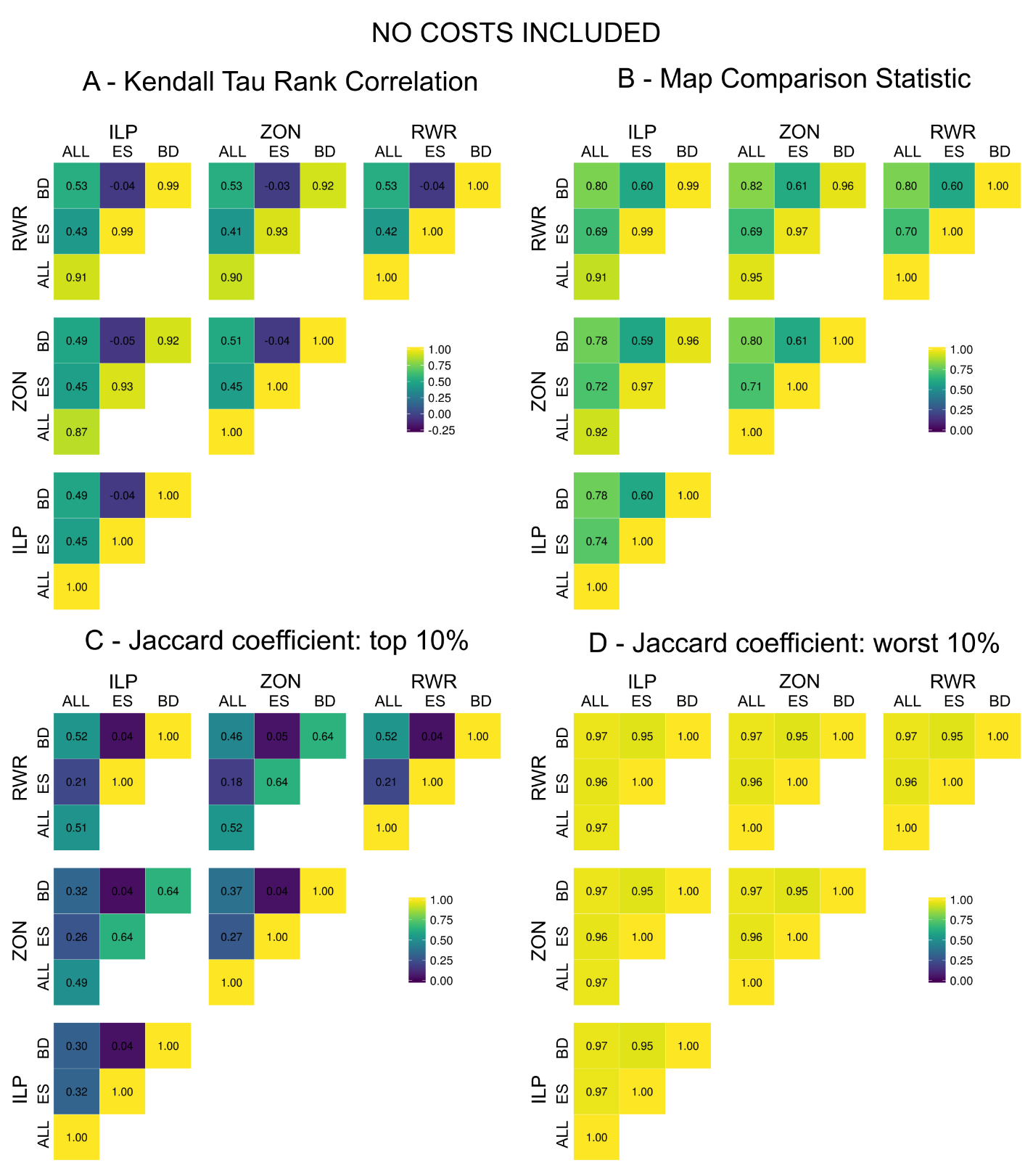
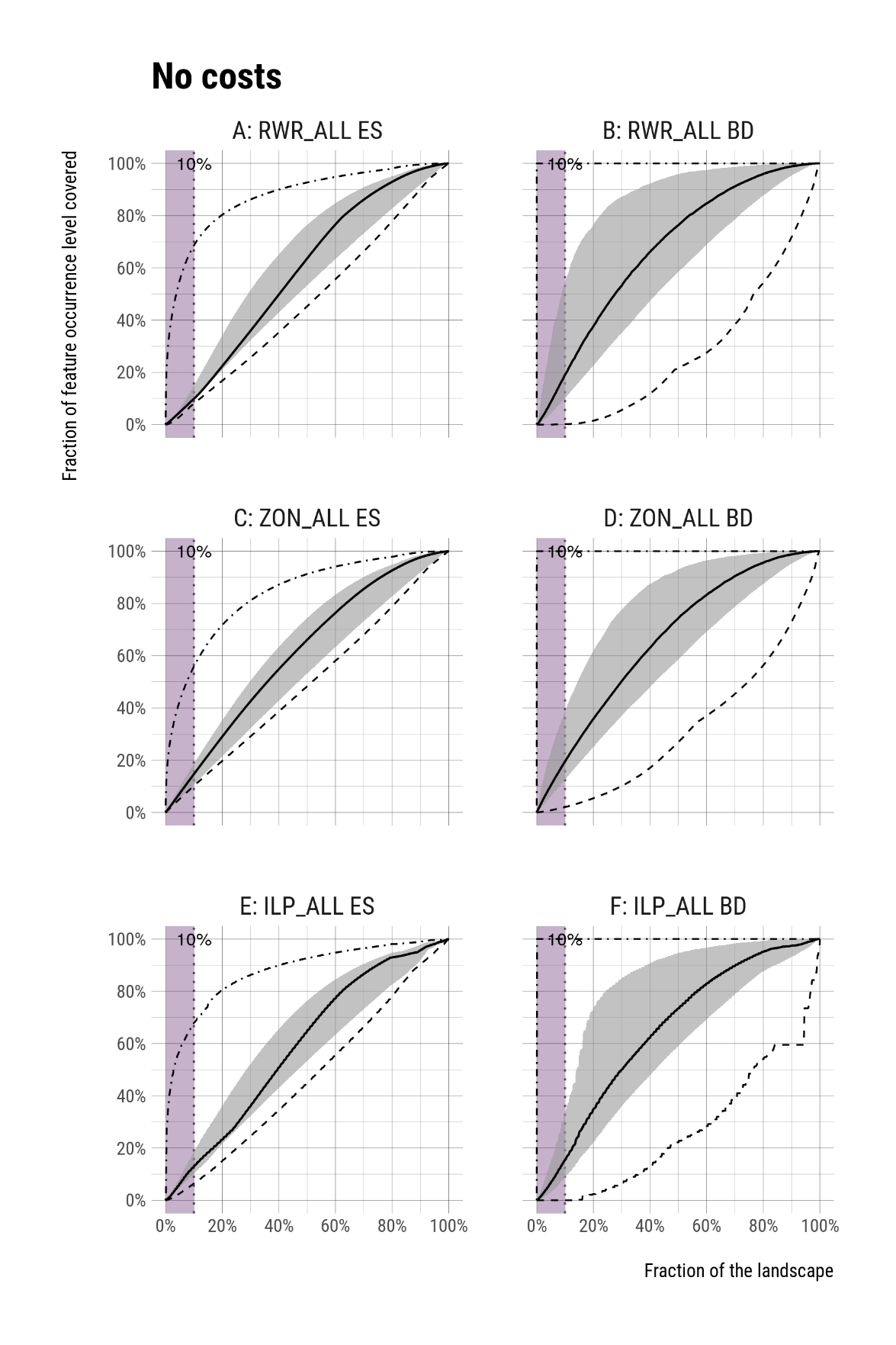


Figure 6.



# Tables

**Table 1.** Spatially explicit datasets used in the study.

**Dataset Group Description Unit Temporal Source  
 coverage**

**Ecosystem services**

Climate ES Response of terrestrial carbon Mg / C / ha 2006 Schulp et al.

regulation balance to land use change scenarios. ⁠ (2008)

Erosion ES Protection of land cover against Ton / ha 2000 – 2030 Pérez-Soba   
prevention erosion in erosion prone areas. et al. (2010)

Flood ES Water retention capacity. Index (relative flood flows) 2007 – 2011 Stürck et al.  
regulation regulation of land use and (2014)

soil on river high flows)

Heritage: ES A cultural heritage index that is used Index 2000 – 2015 Tieskens et al.  
agricultural to show the spatial distribution of (submitted)  
landscapes the overall cultural heritage index

scores in agricultural land.

Heritage: ES A cultural heritage index that is used Index 2000 – 2015 Tieskens et al.  
 to show the spatial distribution of (submitted)  
forests the overall cultural heritage index

scores in forests.

Pollination flows ES Unmanaged pollinators that live in Index (the ratio between 2000 Serna-Chavez

suitable natural and semi-natural the proportion of benefiting et al. (2014)

habitats provide pollination services areas located within the flow   
 especially to near croplands. area and the total benefiting

areas)

Tourism ES Supply of assets for tourism Index 1999-2009 Van Berkel et al.

supported by ecosystems. (2011)

Wild food ES Species richness of wild edible plants, Species richness of vascular 1999 – 2012 Schulp et al.   
provisioning mushrooms and game (supply) and plants (2014)

demand of wild food.

Wood ES High-resolution wood production 1000 m3 / pixel Average of Verkerk et al.  
production maps for European forests. 2000-2010 (2015)

**Biodiversity features**

European BD Species-specific expert-based Percentage of habitat in the 1997 – 2013 Thuiller et al

terrestrial distribution models for 164 mammal, cell (primary + non-primary (2015)

vertebrates 404 bird, 83 amphibian, and 112 habitat)

reptile species. See Table S1 for a

complete listing.

**Table 2.** Performancestatistics of variants RWR\_ALL, ZON\_ALL and ILP\_ALL for the best 10% of the solutions (see also **Fig. 6**). Prioritizations are based on both feature groups (ALL), but statistics are also reported for both feature groups (ES and BD) separately. The values describe the percentage over all features in a given feature group.

**RWR** **ZON** **ILP**

**ALL** ES (ALL) BD (ALL) **ALL** ES (ALL) BD (ALL) **ALL** ES (ALL) BD (ALL)

**min** **0.1%** 8.0% 0.1% **2.0%** 10.1% 2.0% **0.0%** 6.4% 0.0%

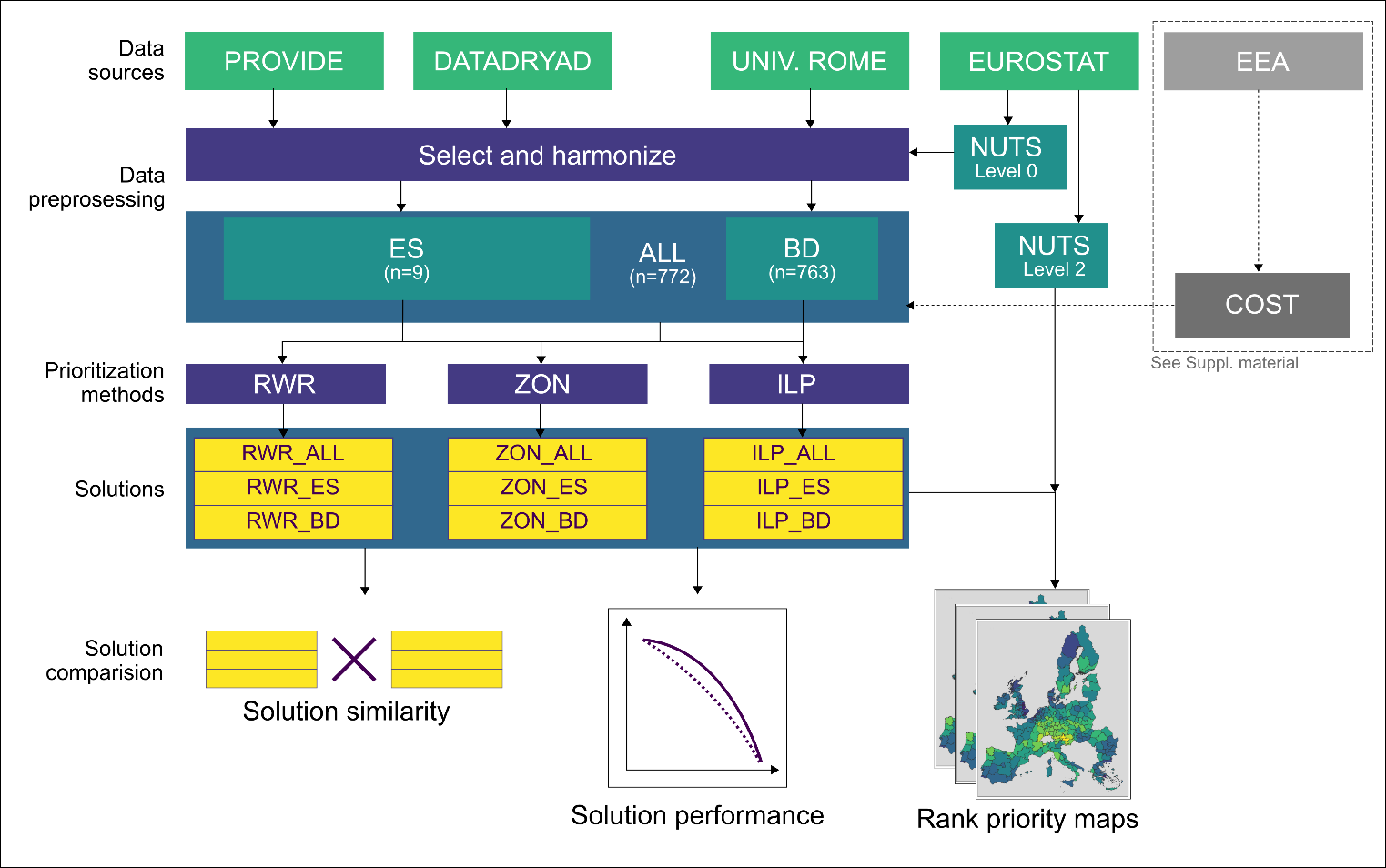
**median** **18.5%** 9.8% 18.9% **19.1%** 14.5% 19.4% **15.3%** 12.8% 15.4%

**mean** **34.7%** 17.2% 34.9% **30.6%** 18.5% 30.8% **25.4%** 18.9% 25.5%

**max** **100.0%** 68.4% 100.0% **100.0%** 55.6% 100.0% **100.0%** 67.6% 100.0%

# Appendix

Figure S1.



**Figure S1.** Schematics of the study workflow.

Table S1. Biodiversity features (n=759) used in the prioritization analyses.

|  |
| --- |
| **Amphibians** |
| Alytes cisternasii |
| Alytes dickhilleni |
| Alytes muletensis |
| Alytes obstetricans |
| Atylodes genei |
| Bombina bombina |
| Bombina pachypus |
| Bombina variegata |
| Bufo bufo |
| Calotriton arnoldi |
| Calotriton asper |
| Chioglossa lusitanica |
| Discoglossus galganoi |
| Discoglossus jeanneae |
| Discoglossus montalentii |
| Discoglossus pictus |
| Discoglossus sardus |
| Epidalea calamita |
| Euproctus montanus |
| Euproctus platycephalus |
| Hyla arborea |
| Hyla intermedia |
| Hyla meridionalis |
| Hyla sarda |
| Lissotriton boscai |
| Lissotriton helveticus |
| Lissotriton italicus |
| Lissotriton montandoni |
| Lissotriton vulgaris |
| Lyciasalamandra helverseni |
| Lyciasalamandra luschani |
| Mesotriton alpestris |
| Pelobates cultripes |
| Pelobates fuscus |
| Pelobates syriacus |
| Pelodytes ibericus |
| Pelodytes punctatus |
| Pelophylax bedriagae |
| Pelophylax bergeri |
| Pelophylax cerigensis |
| Pelophylax cretensis |
| Pelophylax epeirotcus |
| Pelophylax esculentus |
| Pelophylax grafi |
| Pelophylax hispanicus |
| Pelophylax kurtmuelleri |
| Pelophylax lessonae |
| Pelophylax perezi |
| Pelophylax ridibundus |
| Pleurodeles waltl |
| Proteus anguinus |
| Pseudepidalea balearica |
| Pseudepidalea sicula |
| Pseudepidalea variabilis |
| Pseudepidalea viridis |
| Rana arvalis |
| Rana dalmatina |
| Rana graeca |
| Rana iberica |
| Rana italica |
| Rana latastei |
| Rana pyrenaica |
| Rana temporaria |
| Salamandra atra |
| Salamandra corsica |
| Salamandra lanzai |
| Salamandra salamandra |
| Salamandrina perspicillata |
| Salamandrina terdigitata |
| Speleomantes ambrosii |
| Speleomantes flavus |
| Speleomantes imperialis |
| Speleomantes italicus |
| Speleomantes sarrabusensis |
| Speleomantes strinatii |
| Speleomantes supramontis |
| Triturus carnifex |
| Triturus cristatus |
| Triturus dobrogicus |
| Triturus karelinii |
| Triturus macedonicus |
| Triturus marmoratus |
| Triturus pygmaeus  **Birds** |
| Accipiter brevipes |
| Acrocephalus agricola |
| Acrocephalus arundinaceus |
| Acrocephalus dumetorum |
| Acrocephalus melanopogon |
| Acrocephalus paludicola |
| Acrocephalus palustris |
| Acrocephalus schoenobaenus |
| Acrocephalus scirpaceus |
| Actitis hypoleucos |
| Aegithalos caudatus |
| Aegolius funereus |
| Aegypius monachus |
| Alauda arvensis |
| Alca torda |
| Alcedo atthis |
| Alectoris barbara |
| Alectoris chukar |
| Alectoris graeca |
| Alectoris rufa |
| Anas acuta |
| Anas clypeata |
| Anas crecca |
| Anas penelope |
| Anas platyrhynchos |
| Anas querquedula |
| Anas strepera |
| Anser anser |
| Anser brachyrhynchus |
| Anser erythropus |
| Anser fabalis |
| Anthus campestris |
| Anthus cervinus |
| Anthus petrosus |
| Anthus pratensis |
| Anthus spinoletta |
| Anthus trivialis |
| Apus apus |
| Apus caffer |
| Apus melba |
| Apus pallidus |
| Aquila adalberti |
| Aquila chrysaetos |
| Aquila clanga |
| Aquila heliaca |
| Aquila pomarina |
| Ardea cinerea |
| Ardea purpurea |
| Ardeola ralloides |
| Arenaria interpres |
| Asio flammeus |
| Asio otus |
| Athene noctua |
| Aythya ferina |
| Aythya fuligula |
| Aythya marila |
| Aythya nyroca |
| Bombycilla garrulus |
| Bonasa bonasia |
| Botaurus stellaris |
| Branta bernicla |
| Branta leucopsis |
| Bubo bubo |
| Bubulcus ibis |
| Bucanetes githagineus |
| Bucephala clangula |
| Burhinus oedicnemus |
| Buteo buteo |
| Buteo lagopus |
| Buteo rufinus |
| Calandrella brachydactyla |
| Calandrella rufescens |
| Calcarius lapponicus |
| Calidris canutus |
| Calidris maritima |
| Calidris minuta |
| Calidris temminckii |
| Calonectris diomedea |
| Caprimulgus europaeus |
| Caprimulgus ruficollis |
| Carduelis cannabina |
| Carduelis carduelis |
| Carduelis chloris |
| Carduelis flammea |
| Carduelis flavirostris |
| Carduelis hornemanni |
| Carduelis spinus |
| Carpodacus erythrinus |
| Cepphus grylle |
| Cercotrichas galactote |
| Certhia familiaris |
| Cettia cetti |
| Charadrius alexandrinus |
| Charadrius dubius |
| Charadrius hiaticula |
| Charadrius morinellus |
| Chersophilus duponti |
| Chlidonias hybridus |
| Chlidonias leucopterus |
| Chlidonias niger |
| Ciconia ciconia |
| Ciconia nigra |
| Cinclus cinclus |
| Circaetus gallicus |
| Circus aeruginosus |
| Circus cyaneus |
| Circus macrourus |
| Circus pygargus |
| Cisticola juncidis |
| Clamator glandarius |
| Clangula hyemalis |
| Coccothraustes coccothraustes |
| Columba livia |
| Columba oenas |
| Coracias garrulus |
| Corvus corax |
| Corvus corone |
| Corvus frugilegus |
| Corvus monedula |
| Coturnix coturnix |
| Crex crex |
| Cuculus canorus |
| Cuculus saturatus |
| Cyanopica cyana cyanus |
| Cygnus cygnus |
| Cygnus olor |
| Delichon urbica |
| Dendrocopos leucotos |
| Dendrocopos major |
| Dendrocopos medius |
| Dendrocopos minor |
| Dendrocopos syriacus |
| Dryocopus martius |
| Egretta alba |
| Egretta garzetta |
| Elanus caeruleus |
| Emberiza aureola |
| Emberiza caesia |
| Emberiza cia |
| Emberiza cineracea |
| Emberiza cirlus |
| Emberiza citrinella |
| Emberiza hortulana |
| Emberiza melanocephala |
| Emberiza pusilla |
| Emberiza rustica |
| Emberiza schoeniclus |
| Eremophila alpestris |
| Erithacus rubecula |
| Falco biarmicus |
| Falco cherrug |
| Falco columbarius |
| Falco eleonorae |
| Falco naumanni |
| Falco peregrinus |
| Falco rusticolus |
| Falco subbuteo |
| Falco tinnunculus |
| Falco vespertinus |
| Ficedula albicollis |
| Ficedula hypoleuca |
| Ficedula parva |
| Ficedula semitorquata |
| Fratercula arctica |
| Fringilla montifringilla |
| Fulica atra |
| Fulica cristata |
| Fulmarus glacialis |
| Galerida cristata |
| Galerida theklae |
| Gallinago gallinago |
| Gallinago media |
| Gallinula chloropus |
| Garrulus glandarius |
| Gavia arctica |
| Gavia immer |
| Gavia stellata |
| Gelochelidon nilotica |
| Glareola nordmanni |
| Glareola pratincola |
| Glaucidium passerinum |
| Grus grus |
| Gypaetus barbatus |
| Gyps fulvus |
| Haematopus ostralegus |
| Halcyon smyrnensis |
| Haliaeetus albicilla |
| Hieraaetus fasciatus |
| Hieraaetus pennatus |
| Himantopus himantopus |
| Hippolais icterina |
| Hippolais olivetorum |
| Hippolais pallida |
| Hippolais polyglotta |
| Hirundo daurica |
| Hirundo rustica |
| Hoplopterus spinosus |
| Hydrobates pelagicus |
| Ixobrychus minutus |
| Jynx torquilla |
| Lagopus lagopus |
| Lagopus mutus |
| Lanius collurio |
| Lanius excubitor |
| Lanius meridionalis |
| Lanius minor |
| Lanius nubicus |
| Lanius senator |
| Larus argentatus |
| Larus audouinii |
| Larus cachinnans |
| Larus canus |
| Larus fuscus |
| Larus genei |
| Larus marinus |
| Larus melanocephalus |
| Larus minutus |
| Larus ridibundus |
| Limicola falcinellus |
| Limosa lapponica |
| Limosa limosa |
| Locustella fluviatilis |
| Locustella luscinioides |
| Locustella naevia |
| Loxia curvirostra |
| Loxia leucoptera |
| Loxia pytyopsittacus |
| Loxia scotica |
| Lullula arborea |
| Luscinia luscinia |
| Luscinia megarhynchos |
| Luscinia svecica |
| Lymnocryptes minimus |
| Marmaronetta angustirostris |
| Melanitta fusca |
| Melanitta nigra |
| Melanocorypha calandra |
| Mergus albellus |
| Mergus merganser |
| Mergus serrator |
| Merops apiaster |
| Miliaria calandra |
| Milvus migrans |
| Milvus milvus |
| Monticola saxatilis |
| Monticola solitarius |
| Montifringilla nivalis |
| Morus bassanus |
| Motacilla alba |
| Motacilla cinerea |
| Motacilla citreola |
| Motacilla flava |
| Muscicapa striata |
| Neophron percnopterus |
| Netta rufina |
| Nucifraga caryocatactes |
| Numenius arquata |
| Numenius phaeopus |
| Nyctea scandiaca |
| Nycticorax nycticorax |
| Oceanodroma castro |
| Oceanodroma leucorhoa |
| Oenanthe hispanica |
| Oenanthe isabellina |
| Oenanthe leucura |
| Oenanthe oenanthe |
| Oenanthe pleschanka |
| Oriolus oriolus |
| Otis tarda |
| Otus scops |
| Oxyura leucocephala |
| Pandion haliaetus |
| Panurus biarmicus |
| Parus caeruleus |
| Parus cinctus |
| Parus cristatus |
| Parus lugubris |
| Parus major |
| Parus montanus |
| Parus palustris |
| Passer domesticus |
| Passer hispaniolensis |
| Passer italiae |
| Passer montanus |
| Pelecanus crispus |
| Pelecanus onocrotalus |
| Perisoreus infaustus |
| Pernis apivorus |
| Petronia petronia |
| Phalaropus lobatus |
| Phalocrocorax carbo |
| Phalocrocorax pygmaeus |
| Phasianus colchicus |
| Philomachus pugnax |
| Phoenicopterus roseus |
| Phoenicurus ochruros |
| Phoenicurus phoenicurus |
| Phylloscopus bonelli |
| Phylloscopus borealis |
| Phylloscopus collybita |
| Phylloscopus sibilatrix |
| Phylloscopus trochiloides |
| Phylloscopus trochilus |
| Pica pica |
| Picoides tridactylus |
| Picus canus |
| Picus viridis |
| Pinicola enucleator |
| Platalea leucorodia |
| Plectrophenax nivalis |
| Plegadis falcinellus |
| Pluvialis apricaria |
| Podiceps auritus |
| Podiceps cristatus |
| Podiceps grisegena |
| Podiceps nigricollis |
| Porphyrio porphyrio |
| Porzana parva |
| Porzana porzana |
| Porzana pusilla |
| Prunella collaris |
| Prunella modularis |
| Pterocles alchata |
| Pterocles orientalis |
| Ptyonoprogne rupestris |
| Puffinus mauretanicus |
| Puffinus puffinus |
| Puffinus yelkouan |
| Pyrrhocorax graculus |
| Pyrrhocorax pyrrhocorax |
| Pyrrhula pyrrhula |
| Rallus aquaticus |
| Recurvirostra avosetta |
| Regulus ignicapillus |
| Regulus regulus |
| Remiz pendulinus |
| Riparia riparia |
| Rissa tridactyla |
| Saxicola rubetra |
| Saxicola torquata |
| Scolopax rusticola |
| Serinus citrinella |
| Serinus serinus |
| Sitta europaea |
| Sitta krueperi |
| Sitta neumayer |
| Sitta whiteheadi |
| Somateria mollissima |
| Stercorarius longicaudus |
| Stercorarius parasiticus |
| Stercorarius skua |
| Sterna albifrons |
| Sterna bengalensis |
| Sterna caspia |
| Sterna dougallii |
| Sterna hirundo |
| Sterna paradisaea |
| Sterna sandvicensis |
| Streptopelia decaocto |
| Streptopelia turtur |
| Strix aluco |
| Strix nebulosa |
| Strix uralensis |
| Sturnus roseus |
| Sturnus unicolor |
| Sturnus vulgaris |
| Surnia ulula |
| Sylvia atricapilla |
| Sylvia borin |
| Sylvia cantillans |
| Sylvia communis |
| Sylvia conspicillata |
| Sylvia curruca |
| Sylvia hortensis |
| Sylvia melanocephala |
| Sylvia nisoria |
| Sylvia rueppelli |
| Sylvia sarda |
| Sylvia undata |
| Tachybaptus ruficollis |
| Tadorna ferruginea |
| Tadorna tadorna |
| Tarsiger cyanurus |
| Tetrao urogallus |
| Tetrax tetrax |
| Tichodroma muraria |
| Tringa erythropus |
| Tringa glareola |
| Tringa nebularia |
| Tringa ochropus |
| Tringa stagnatilis |
| Tringa totanus |
| Turdus iliacus |
| Turdus merula |
| Turdus philomelos |
| Turdus pilaris |
| Turdus torquatus |
| Turdus viscivorus |
| Turnix sylvatica |
| Tyto alba |
| Upupa epops |
| Uria lomvia |
| Vanellus vanellus |
| Xenus cinereus |
| **Mammals** |
| Acomys minous |
| Alces alces |
| Alopex lagopus |
| Apodemus agrarius |
| Apodemus alpicola |
| Apodemus epimelas |
| Apodemus flavicollis |
| Apodemus mystacinus |
| Apodemus sylvaticus |
| Apodemus uralensis |
| Apodemus witherbyi |
| Arvicola amphibius |
| Arvicola sapidus |
| Arvicola scherman |
| Atelerix algirus |
| Barbastella barbastellus |
| Bison bonasus |
| Canis aureus |
| Capra ibex |
| Capra pyrenaica |
| Capreolus capreolus |
| Chionomys nivalis |
| Cricetulus migratorius |
| Cricetus cricetus |
| Crocidura leucodon |
| Crocidura pachyura |
| Crocidura russula |
| Crocidura sicula |
| Crocidura suaveolens |
| Crocidura zimmermanni |
| Dama dama |
| Dinaromys bogdanovi |
| Dryomys nitedula |
| Eliomys quercinus |
| Eptesicus bottae |
| Eptesicus nilsonii |
| Eptesicus serotinus |
| Erinaceus europaeus |
| Erinaceus roumanicus |
| Felis silvestris |
| Galemys pyrenaicus |
| Genetta genetta |
| Glis glis |
| Gulo gulo |
| Hystrix cristata |
| Lemmus lemmus |
| Lepus capensis |
| Lepus castroviejoi |
| Lepus corsicanus |
| Lepus europaeus |
| Lepus granatensis |
| Lepus timidus |
| Lutra lutra |
| Lynx pardinus |
| Martes foina |
| Martes martes |
| Meles meles |
| Meriones tristami |
| Mesocricetus newtoni |
| Micromys minutus |
| Microtus agrestis |
| Microtus arvalis |
| Microtus bavaricus |
| Microtus brachycercus |
| Microtus cabrerae |
| Microtus duodecimcostatus |
| Microtus felteni |
| Microtus gerbei |
| Microtus guentheri |
| Microtus levis |
| Microtus liechtesteini |
| Microtus lusitanicus |
| Microtus multiplex |
| Microtus oeconomus |
| Microtus savii |
| Microtus subterraneus |
| Microtus tatricus |
| Microtus thomasi |
| Miniopterus schreibersi |
| Mus macedonicus |
| Mus musculus |
| Mus spicilegus |
| Mus spretus |
| Muscardinus avellanarius |
| Mustela erminea |
| Mustela eversmanii |
| Mustela lutreola |
| Mustela nivalis |
| Mustela putorius |
| Myodes glareolus |
| Myodes rufocanus |
| Myodes rutilus |
| Myomimus roachi |
| Myopus schisticolor |
| Myotis alcathoe |
| Myotis aurascens |
| Myotis bechsteinii |
| Myotis blythii |
| Myotis brandtii |
| Myotis capaccinii |
| Myotis dasycneme |
| Myotis daubentonii |
| Myotis emarginatus |
| Myotis myotis |
| Myotis mystacinus |
| Myotis nattereri |
| Myotis punicus |
| Neomys anomalus |
| Neomys fodiens |
| Nyctalus lasiopterus |
| Nyctalus leisleri |
| Nyctalus noctula |
| Oryctolagus cuniculus |
| Ovis aries |
| Pipistrellus kuhlii |
| Pipistrellus nathusii |
| Pipistrellus pipistrellus |
| Pipistrellus pygmaeus |
| Pipistrellus savii |
| Plecotus auritus |
| Plecotus austriacus |
| Plecotus kolombatovici |
| Plecotus macrobullaris |
| Plecotus sardus |
| Pteromys volans |
| Rhinolophus blasii |
| Rhinolophus euryale |
| Rhinolophus ferrumequinum |
| Rhinolophus hipposideros |
| Rhinolophus mehelyi |
| Rupicapra rupicapra |
| Sciurus anomalus |
| Sciurus vulgaris |
| Sicista betulina |
| Sicista severtzovi |
| Sicista subtilis |
| Sorex alpinus |
| Sorex antinorii |
| Sorex araneus |
| Sorex caecutiens |
| Sorex coronatus |
| Sorex granarius |
| Sorex isodon |
| Sorex minutissimus |
| Sorex minutus |
| Sorex samniticus |
| Spalax graecus |
| Spalax leucodon |
| Spalax nehringi |
| Spermophilus citellus |
| Spermophilus suslicus |
| Suncus etruscus |
| Sus scrofa |
| Tadarida teniotis |
| Talpa caeca |
| Talpa europaea |
| Talpa levantis |
| Talpa occidentalis |
| Talpa romana |
| Talpa stankovici |
| Ursus arctos |
| Vespertilio murinus |
| Vormela peregusna |
| Vulpes vulpes |
| Ablepharus kitaibelii |
| Acanthodactylus erythrurus |
| **Reptiles** |
| Algyroides fitzingeri |
| Algyroides marchi |
| Algyroides moreoticus |
| Algyroides nigropunctatus |
| Anatolacerta anatolica |
| Anatolacerta oertzeni |
| Anguis cephallonica |
| Anguis fragilis |
| Archaeolacerta bedriagae |
| Blanus cinereus |
| Blanus strauchi |
| Chalcides bedriagai |
| Chalcides chalcides |
| Chalcides ocellatus |
| Chalcides striatus |
| Chamaeleo africanus |
| Chamaeleo chamaeleon |
| Coronella austriaca |
| Coronella girondica |
| Cyrtopodion kotschyi |
| Darevskia praticola |
| Dolichophis caspius |
| Dolichophis jugularis |
| Eirenis modestus |
| Elaphe quatuorlineata |
| Elaphe sauromates |
| Emys orbicularis |
| Emys trinacris |
| Eremias arguta |
| Eryx jaculus |
| Euleptes europaea |
| Eumeces schneideri |
| Hellenolacerta graeca |
| Hemidactylus turcicus |
| Hemorrhois hippocrepis |
| Hemorrhois nummifer |
| Hierophis gemonensis |
| Hierophis gyarosensis |
| Hierophis viridiflavus |
| Iberolacerta aranica |
| Iberolacerta aurelioi |
| Iberolacerta bonnali |
| Iberolacerta cyreni |
| Iberolacerta galani |
| Iberolacerta horvathi |
| Iberolacerta martinezricai |
| Iberolacerta monticola |
| Lacerta agilis |
| Lacerta bilineata |
| Lacerta schreiberi |
| Lacerta trilineata |
| Lacerta viridis |
| Laudakia stellio |
| Macroprotodon brevis |
| Macroprotodon cucullatus |
| Macroprotodon mauritanicus |
| Macrovipera schweizeri |
| Malpolon monspessulanus |
| Mauremys leprosa |
| Mauremys rivulata |
| Montivipera xanthina |
| Natrix maura |
| Natrix tesselleta |
| Ophiomorus punctatissimus |
| Ophisops elegans |
| Parvilacerta parva |
| Platyceps collaris |
| Platyceps najadum |
| Podarcis bocagei |
| Podarcis carbonelli |
| Podarcis erhardii |
| Podarcis filfolensis |
| Podarcis gaigeae |
| Podarcis hispanica |
| Podarcis lilfordi |
| Podarcis melisellensis |
| Podarcis milensis |
| Podarcis muralis |
| Podarcis peloponnesiaca |
| Podarcis pityusensis |
| Podarcis raffonei |
| Podarcis sicula |
| Podarcis taurica |
| Podarcis tiliguerta |
| Podarcis vaucheri |
| Podarcis wagleriana |
| Psammodromus hispanicus |
| Psammodromus jeanneae |
| Psammodromus manuelae |
| Pseudopus apodus |
| Rhinechis scalaris |
| Tarentola mauritanica |
| Telescopus fallax |
| Testudo graeca |
| Testudo hermanni |
| Testudo marginata |
| Timon lepidus |
| Trachylepis aurata |
| Trionyx triunguis |
| Typhlops vermicularis |
| Vipera ammodytes |
| Vipera aspis |
| Vipera berus |
| Vipera latastei |
| Vipera renardi |
| Vipera seoanei |
| Vipera ursinii |
| Zamenis lineatus |
| Zamenis longissimus |
| Zamenis situla |
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