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Matches and mismatches between national and EU-wide priorities: Examining the Natura 2000 network in vertebrate species conservation

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ABSTRACT

The Natura 2000 (N2k) is a network of protected areas, established to implement the Birds and the Habitats Directives of the European Union (EU) with the goal of conservation irrespective of national boundaries. We provide the first assessment of the whole terrestrial N2k using spatial prioritizations, and high-resolution vertebrate species distribution data. First, we quantified species' representation in the network, and compared it against outcomes of hypothetical optimal planning scenarios at the EU, member state, and biogeographical levels. Second, we examined the spatial configuration of N2k sites and same-sized hypothetical top priority sites based on the three planning scenarios. We found that N2k covered all vertebrate directive species, and the coverage was significantly better than with a random allocation of sites. We observed substantial differences in representation between taxa, followed by the fact that N2k succeeded better in covering threatened and directive species than non-directive species. The current species representation in N2k was closer to optimal allocations done at member states' or biogeographical levels than the EU-wide allocation. Furthermore, the N2k sites overlapped more with the EU-wide allocation and they were more evenly distributed across the EU compared to sites in all hypothetical optimal allocations. Finally, we found that the biogeographical scenario covered well the ranges of habitats directive species, following the biogeographical approach taken by the EU in the Habitats Directive. Our results show that despite N2k being moderately successful, there is substantial effectiveness to be gained from member state collaboration via potential expansions or complementary conservation policies.

1. Introduction

The European Union (EU) has been active in biodiversity conservation through the establishment of the Natura 2000 network (N2k). The N2k consists of two types of sites designated on the basis of the Birds Directive (79/409/EEC) and the Habitats Directive (92/43/EEC) (Table 1). Currently, there are more than 27,000 sites, covering 18% of the EU's land area (EEA, 2012).

The aim of the N2k to protect biodiversity "irrespective of national or political boundaries" clearly implies that site designation should be developed using EU-level criteria and planning. The selection of Sites of Community Interest (SCIs) for species and habitats listed in the Habitats directive is a cooperative process between the member states and the Commission (European Commission, 2014a, 2014b; Table 1). However, Special Protection Areas (SPAs) for birds listed in the Birds Directive are selected by the member states with no commonly agreed EU-wide criteria (Evans, 2012; Gruber et al., 2012). As a result, the designation of sites has often been criticized as non-systematic, lacking quantitative site selection criteria, and ignoring complementarity and other principles of systematic conservation planning (SCP, Margules and Pressey, 2000; Apostolopoulou and Pantis, 2009; Culmsee et al., 2014; Gaston et al., 2008; Hochkirch et al., 2013; Kati et al., 2015). Additionally, N2k

Abbreviations: N2k, the Natura 2000 network; SPA, Special Protection Area; SCIs, Sites of Community Interest.

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Table 1
The two nature directives (Birds and Habitats Directives) are at the core of the continent-wide biodiversity conservation strategy, guided by the European Commission and implemented by the member states (European Commission, 2014a, 2014b). Note, that SPAs are also designated for regularly occurring migratory species not listed in Annex I (Birds Directive Article 4), but we considered only Annex I (Birds Directive) species in our prioritizations.

Annex	Year of origin/the newest version of the directive	Biodiversity feature to be protected	Conservation target	Site selection process for Natura 2000	Natura 2000 sites
Annex I Birds Directive (BD)	1979/2009 79/409/EEC 2009/147/EC	Bird species and their habitats	Protection of habitats for endangered and migratory bird species	SPAs are selected directly by the member states with no agreed EU criteria for site selection. However, the process should be based on scientific criteria. Finally, the European Commission determines if the designated sites are sufficient.	Special Protection Areas (SPAs)
Annex I Habitats Directive (HD)	1994/2006 92/43/EEC 2006/105/EC	Habitats	Conservation of habitat types of European interest	1. Member states' proposals for sites, based on standard selection criteria specified in the Directive 2. Biogeographical seminars are arranged by the European Commission, aiming to evaluate if sufficient high-quality sites have been proposed by each member state 3. Member states designate all of these sites as Special Areas of Conservation	Sites of Community Interest (SCIs)/Special Areas for Conservation (SACs)
Annex II Habitats Directive (HD)	1994/2006 92/43/EEC 2006/105/EC	Species	For species listed in Annex II core areas of their habitat must be protected and managed under the N2k		SCIs/SACs
Annex IV Habitats Directive (HD)	1994/2006 92/43/EEC 2006/105/EC	Species	A strict protection regime must be applied across species entire natural range within the EU, both within and outside N2k sites		SCIs/SACs

as an effective conservation strategy has been debated (D'Amen et al., 2013; Dimitrakopoulos et al., 2004; Grodzinska-Jurczak and Cent, 2011; Pullin et al., 2009; Wamelink et al., 2013). Each country has its own distinct political history and a pre-existing national protected area network. Therefore, many N2k sites overlap with previously established national protected areas (EEA, 2012).

Despite the hundreds of publications addressing N2k matters (Popescu et al., 2014), the effectiveness and representativeness of the network are still inadequately understood and the studies are often taxonomically or geographically biased (Araujo et al., 2007; Chiarucci et al., 2008; EEA, 2012; Jantke et al., 2011; Lison et al., 2015; Maiorano et al., 2007, 2015; Verovnik et al., 2011). Overall, studies have found that some species rich areas or species have been missed by the network (Abellan et al., 2011; Albuquerque et al., 2013; Bagella et al., 2013; Gruber et al., 2012; Thuiller et al., 2015; Trochet and Schmeller, 2013).

While protected area networks seem to currently perform better than random, recent evidence indicates that they are not optimal, and better achievements could be obtained with more coordinated planning (Bladt et al., 2009; Kark et al., 2015; Mazor et al., 2013; Pouzols et al., 2014). Also, global and local priorities coincide only partially (Moilanen and Arponen, 2011; Moilanen et al., 2013). While it is difficult to assess the efficiency of protected areas taking into account all relevant factors (ecological and socio-economical), it is important to understand the potential efficiency loss that arises from planning that divides conservation effort into ecologically arbitrary subunits. This is particularly interesting in the context of the whole N2k network in the EU, since it has never been compared to a theoretically optimal spatial design. Previous studies investigating N2k with systematic planning methods have been at national scales or focused on species groups other than those investigated here (Jantke et al., 2011; Mikkonen and Moilanen, 2013).

Here, we present an EU-wide assessment for N2k using a comparatively high-resolution dataset covering 841 terrestrial vertebrate species. We use spatial prioritizations to assess the present N2k network in addressing the goals of EU legislation and securing vertebrate diversity. We examine whether the species coverage and spatial pattern of the N2k network better reflect a community effort or interests of independent member states. We perform spatial prioritizations separately at the EU and national scales, testing hypothetical planning outcomes at different administrative levels. We also conduct an analysis where an effectively independent prioritization is done for each biogeographical region, as described in the Habitats Directive as regions characterized by distinctive vegetation, climate, and geology (EEA, 2014a). Such a biogeographical approach has previously been taken in the selection process of SCIs.

2. Material and methods

2.1. Data

Our species data are a subset of the species-specific expert-based distribution models described in Maiorano et al. (2013). We focused on vertebrate species that are listed in the EU nature legislation (EIONET, 2014a, 2014b; Tables 1, 2). Accordingly, data were first extracted within the member states (EU28) for 85 amphibians, 141 reptiles, 180 mammals, and 435 birds, and then, a subset of 395 directive species was included in the present analysis. Since the selection processes of SCIs and SPAs differ significantly (see Table 1 for details), we considered Birds directive species (Annex I) and Habitats directive species (Annex II) separately. Finally, we considered Annex IV species (Habitats directive) together with Annex I and II species, because Annex IV species should be protected both in and outside N2k. While there are over 1000 species including also other taxa such as insects and plants listed in the Habitats Directive (EIONET, 2014a), we had data only for amphibians, reptiles, and mammals (Table 2). Birds were

Table 2
Number of species in different groups used in the analyses and Zonation priority scenarios. In parenthesis, there are the percentages of species listed in the Birds and Habitats directives covered by the present data. Note that the same habitats directive species could be listed under both Annex II and Annex IV and thus the Annex II category has an overlap with Annex IV species. Each prioritization scenario was run for each species grouping.

Species distribution data used in the Zonation analyses					
Species groupings	Amphibians	Mammals	Reptiles	Birds	Total
All species	85	180	141	435	841
All directive species (Annexes I, II, IV)	56 (90%)	77 (57%)	81 (69%)	181 (93%)	395
Birds directive species (Annex I only)				181 (93%)	181
Habitats directive species (Annex II only)	28 (78%)	38 (60%)	24 (80%)		90
Non-Annex-I-directive species[a]				254	254
Non-Annex-II-directive species[b]	57	142	117		316

Zonation priority scenarios	Administrative units (n)	Description
EU joint	1	Land area of EU member states considered as a joint planning area
Member states	28	EU member states considered separately (with independent priorities)
Biogeographical regions	9	Biogeographical regions considered separately (with independent priorities)
N2k network	1–28	Hierarchic prioritization analysis to assess the present N2k network
Random	1	Prioritization for each species group was done 100× with random ranking. This provides a baseline expectation for performance.

[a] Includes all birds species covered by the present data that are not listed in the directive (Annex I, BD).
[b] Includes all amphibian, mammal and reptile species covered by the present data not listed in Annex II (HD). Note that this group includes also some Annex IV species.

the most representative group in terms of available data, covering 93% of all species listed in the Birds Directive (Table 2).

The raw species data were available at 300 m resolution for each species. Habitat requirements were used to refine each species' extent of occurrence using an expert-based modeling approach (see Maiorano et al., 2013 for details). Finally, we had data indicating suitable habitat (1) or not (0). To limit computational demands of spatial prioritization, we aggregated this dataset to a 1.5 km resolution by counting the number of suitable 300 m pixels within each 1.5 km pixel, resulting in values between 0.0 and 25.0. The 1.5 km cell size is close to the mean size of N2k sites (EEA, 2012), which enables a fair comparison of hypothetical optimal allocation vs. existing N2k sites (i.e. the difference in effectiveness is not due to higher resolution of prioritization compared to that which could feasibly be implemented). We rasterized the latest version of the N2k network (EEA, 2014b), and since we analyzed birds and habitats directive species separately, we used three versions of the N2k network: all N2k sites, SPAs, and SCIs.

2.2. Conservation priorities

We used the Zonation v4.0 software for spatial prioritizations (Moilanen et al., 2014). Zonation produces a hierarchical prioritization of the landscape based on the occurrence levels of biodiversity features and other data such as costs and connectivity. Zonation ranks cells by iteratively removing the least valuable remaining cell while accounting for generalized complementarity. Analyses were done with the core-area analysis variant, which aims at maintaining high-quality areas for all species. This aim coincides well with the N2k target of retaining the best habitats and preserving all directive species. First, we ran EU-wide prioritizations and hierarchic analyses across N2k sites, enabling a comparison between the present N2k network and optimal priority ranking across the EU (EU joint scenario, Table 1). We used a hierarchic mask of the N2k network in Zonation, which forces the prioritization to first rank the cells across the surrounding landscape and only then to move into the N2k network, thereby enabling analysis of optimal conservation area network expansion (see Moilanen et al., 2014 for further details).

Second, we carried out prioritizations with administrative unit analysis (strong variant of Moilanen and Arponen, 2011), which requires all features to be represented separately in each administrative region (here member state, or biogeographical region) when possible. [The strong analysis variant is in contrast to the weak, which has different weights for features in different administrative areas, but which views distributions of features in the global context rather than in the context of each admin area separately.] Zero weight was given to the global component of administrative unit analysis, effectively meaning that an independent prioritization was done in one go for each member state or biogeographical region in the EU. Thus, alternative prioritizations allowed us to imitate a process where conservation planning is either a pure group effort of the EU or where each country or biogeographical region is independently responsible for the allocation of sites. To assess baseline representation levels, we also evaluated randomization runs, in which cells are ranked randomly without any consideration of occurrence levels of features (Table 1).

2.3. Post-processing analyses

In post-processing, we evaluated vertebrate species coverage in N2k sites against four hypothetical alternatives: (i) maximum coverage possible with random selection of areas, (ii) maximum coverage possible with the same area across the EU, and maximal coverage possible using (iii) member states, and (iv) biogeographical regions as independent sub-units. We replicated this for all taxa and for separate species groups (Table 1). The coverages were compared for all 395 directive species within the top 18.3% of landscape based on each hypothetical prioritization scenario, corresponding to the extent of the N2k network (18.3%). The same comparisons were done for birds directive species within the top 12.5% of landscape and for habitats directive species within the top 14% of landscape, corresponding the extents of the two N2k sub-networks (SPAs and SCIs). By the top priority areas we mean the 18.3%, 12.5% or 14% of the landscape, which maximizes species' representations. Coverage levels were read from performance curve output by Zonation, which reports the remaining proportions of a species' range at all stages of the landscape priority ranking. This procedure allowed evaluating whether the species coverage in the N2k network more closely resembles an optimal EU joint prioritization or a more regionalized one.

We compared the spatial pattern of N2k cells against the same extent of top priority cells in the three hypothetical optimal prioritizations (EU, member state and biogeographical regions). The top priority cells for each prioritization were extracted from output maps of Zonation in ArcGIS, after which the extent of spatial overlaps between the N2k cells and the same-extent top priority area cells was compared.

In previous Zonation studies where effectively independent prioritizations are done in administrative units of different size (Moilanen et al., 2013; Pouzols et al., 2014), an “edge effect”, has been observed, meaning that spatial priorities tend to concentrate near administrative borders due to species distributions and richness gradients that intersect borders: "Complementary" sites that differ most in their species composition tend to be located far away from each other, near borders.

In order to evaluate the degree of edge effect and spatial configuration of the N2k sites and top priority sites by each scenario, we calculated Euclidean distances from each grid cell in the N2k to the closest member state border. The same distance calculations were done also for the top priority cells in the three hypothetical prioritizations (EU joint, member state and biogeographical scenarios).

In addition to analysis of species coverage and spatial pattern, we also investigated how member states rank in terms of overall EU-wide joint conservation priorities. The Zonation output includes a unique rank value for each pixel across the study region. Rank values were compared across countries by calculating average and median pixel-specific priority ranks across each country. Statistical and GIS analyses were conducted with ArcGIS, R, and SPSS, with details described in Appendix A.

3. Results

3.1. Effectiveness of the present N2k

We did not identify any vertebrate species not covered by the N2k, meaning that the network does fulfill its main target of representing all vertebrate directive species. While there were differences in species coverage between the member states (Table A1) we found that the N2k on average covers the ranges of all vertebrate directive species significantly better than random (Fig. 1 panel D, Fig. 2). Nevertheless, the N2k covers a mean of 33.6% of all vertebrate directive species ranges while it could have covered 60.3% with optimally selected areas (Table A2). These general patterns persist regardless of species grouping (Figs. 1, 2, A1, A2) and all differences are significant (Table A3).

Generally, habitats and birds directive species have on average higher coverage than non-directive species in SCIs/SPAs (Figs. 2, A1, Table A2). There are some differences between taxa, with mammals and amphibians being the groups with the presently lowest mean

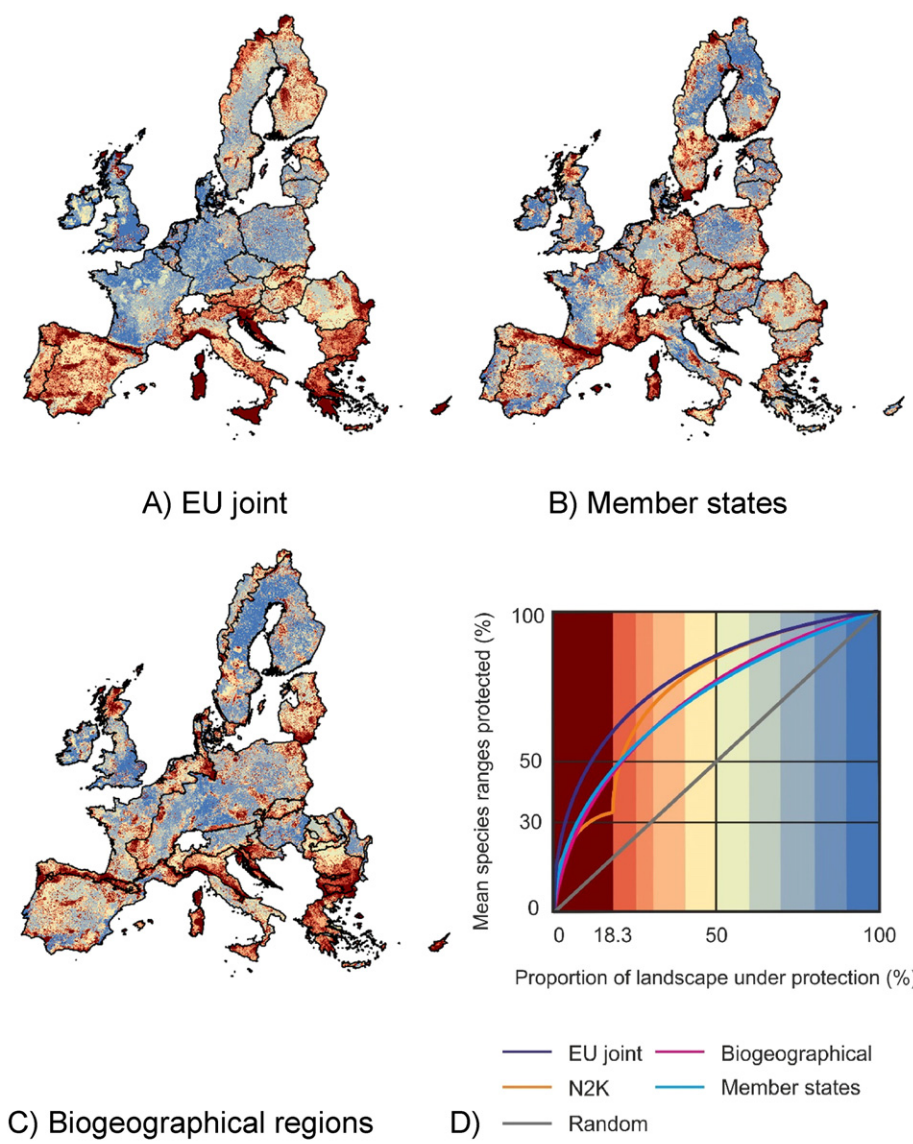

Fig. 1. Priorities for all vertebrate directive species are presented for each hypothetical administrative planning scenario (A, B, or C) with the same color scale (D). Here, areas have been zoned to graded colors based on their priority rank, with highest priorities (top 18.3% of EU area) shown in red. Performance curves (D) are presented for all five prioritization scenarios and they report the mean proportion of vertebrate directive species' ranges at different stages of the landscape ranking. For example, when 18.3% of land is under protection in the N2k scenario, on average 34% of species ranges are covered, while the EU joint scenario can on average cover 60% of species ranges with the same 18.3% of land. (For interpretation of the references to color in this figure legend, the reader is referred to the online version of this chapter.)

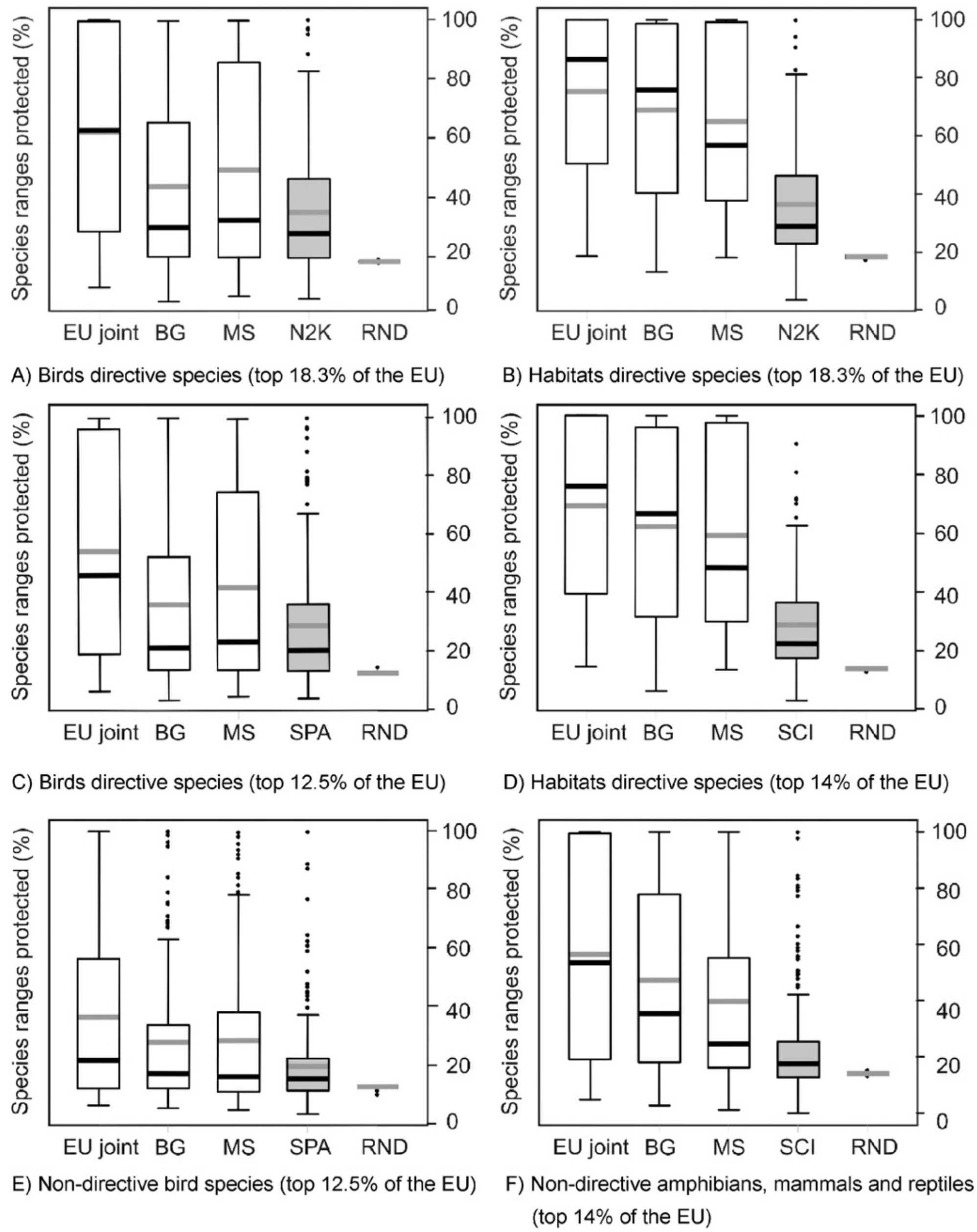

Fig. 2. The proportion of individual species ranges covered in the same extent of area are shown for each prioritization scenario: the EU joint scenario, biogeographical regions (BG), member states (MS), current N2k scenario (N2k, SCI or SPA), and for the random prioritization scenario (RND). Note, that the non-habitats directive species group includes all amphibians, mammals, and reptiles that are not classified as Annex II species under the Habitats directive. Medians are shown as black lines, means as gray lines, and lower and upper quartiles as whiskers with 99% of the data contained between the whiskers. Potential outliers are shown as circles. The percentages compared correspond to each N2k sub-network's extent of area: 18.3% for the coverage of the N2k network in the EU, 12.5% and 14% for SPAs and SCIs, respectively.

range coverage (29.8% and 32.1%) in N2k (Table A2). We found significant differences between the present coverage by N2k and maximum coverage possible with the same area, with reptiles holding the largest potential for increased coverage (Table A2). These patterns become amplified when looking at narrow-range species only (Fig. A3). Different taxa also have different mean range sizes: reptiles and amphibians have significantly (Kruskal–Wallis one way ANOVA, $p < 0.001$) smaller ranges than mammals and birds (Tables A4, A5, A6).

Species range coverage in the N2k generally increases with threat level, as based on the IUCN Red List status (Fig. 3, Tables A7, A8) and decreases with range size (Fig. 4), but with important exceptions. The fraction of range covered by the N2k and species range size are correlated (Spearman coefficient −0.552, significant at the $p < 0.01$ level), as are threat level and range size (Spearman coefficient −0.361, significant at the $p < 0.01$ level). However, there were some threatened vertebrates with low representation in the N2k, even though high coverage could have been achieved in the EU joint scenario (Table A9).

3.2. Prioritization outcomes at different administrative subdivisions

The EU joint scenario, which did not use any subdivision to administrative units, covered a higher fraction of species ranges than the N2k, member states or biogeographical scenarios, and this difference in efficiency was found regardless of species grouping (Figs. 1, 2, Table A2). Instead, when comparing the member states and biogeographical scenarios, there were differences between species groupings in terms of range coverage in the same extent of area (Fig. 2). The biogeographical scenario performed better for species listed in the habitats directive species (median 66.5% species ranges covered) compared to the member states scenario (median 48.1%). Habitats directive species were

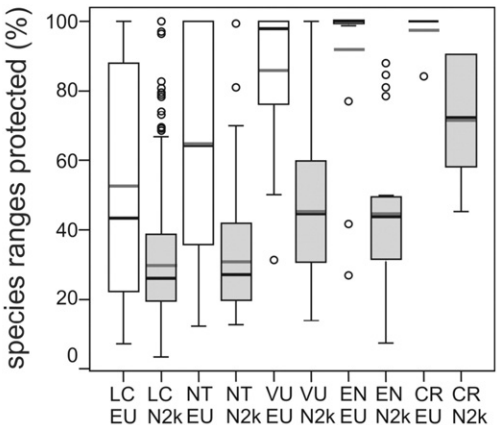

Fig. 3. All vertebrate directive species grouped by their IUCN Red List status (IUCN, 2014) and their ranges protected in the present N2k (N2k, gray boxplots) and maximum coverage possible with a same extent of areas in the EU joint scenario (EU, white boxplots). Abbreviations for IUCN Red List species categories are LC, NT, VU, EN, and CR (LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered). Medians are shown as black lines, means as gray lines, and lower and upper quartiles as whiskers with 99% of the data contained between the whiskers. Potential outliers are shown as circles.

also the only species group whose ranges covered in the biogeographical scenario did not differ significantly at the $p < 0.05$ level from the EU joint scenario (Table A3).

We also found that differences in how administrative units cover rare species might have a significant impact on prioritization outcome. For example, Macaronesia is an independent smallish administrative region with many endemic species occurring there in a locally widespread manner. Therefore, the entire Macaronesia receives high priority in the EU joint prioritization. However, Macaronesian species cannot get high percentages of ranges covered in the biogeographical scenario, because the hypothetical protected area network with the same size as the N2k can only cover 18.3% of land area in each biogeographic region separately, which leads to decreased efficiency of the biogeographical scenario.

3.3. Allocations of sites in administrative scenarios compared to N2k sites

Comparing the spatial configuration of the present N2k to the EU joint scenario for all vertebrate directive species, 33.5% of N2k sites overlap with the top 18.3% cells of the optimal allocation (Fig. 5). In contrast, only 8.7% of N2k sites are located within the 18.3% of the EU that has the lowest-priority for vertebrate conservation. Both the SCI network and N2k for habitats directive species are closer to the optimal allocation than other scenarios. Instead, optimal allocation of sites for

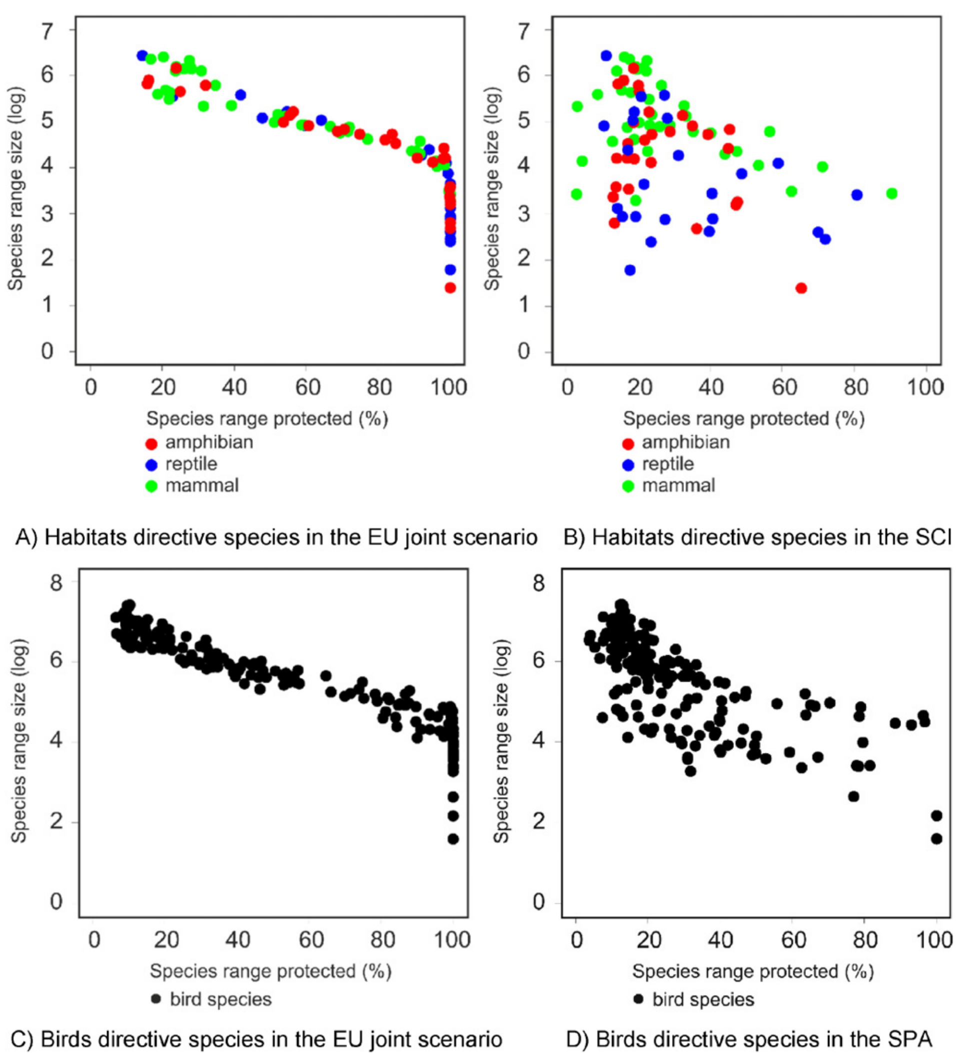

Fig. 4. Habitats and Birds directive species' range sizes (logarithmic scale) are plotted against their range coverage in the current SCI or SPA network (B, D) and in the EU joint scenario (A, C).

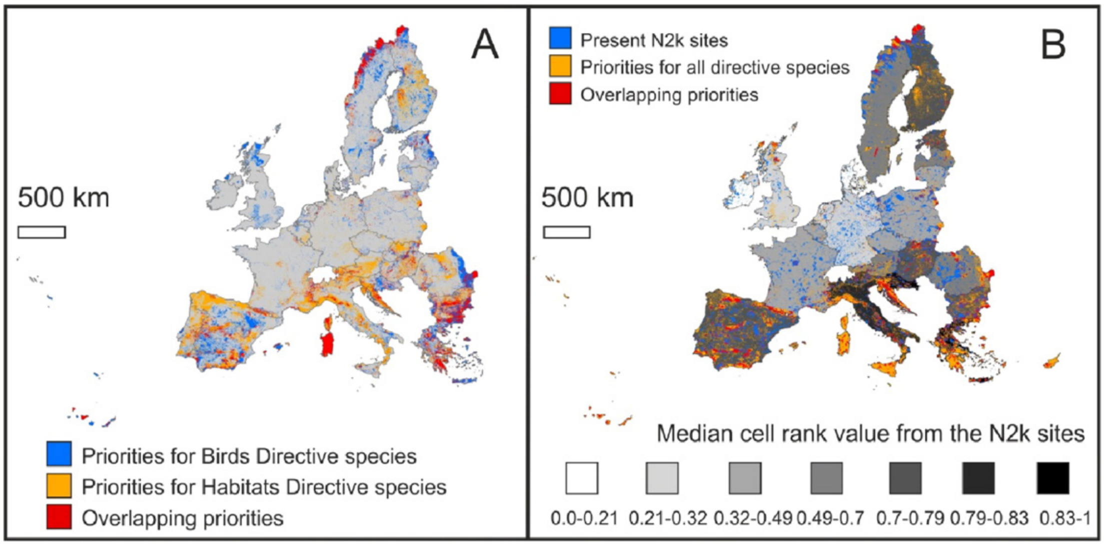

Fig. 5. Panel A shows the priority areas for the Birds directive species and the Habitats directive species in the EU when looking at the top 18.3% of land. Panel B shows the top 18.3% of land for all directive species. Overlapping sites between the EU joint scenario priorities and the current N2k network are shown in red. The present N2k sites that are not included in the top EU-wide priorities based on the present prioritization are shown in blue. The median cell rank values (0–1) for the country-specific N2k networks are shown in gray-scale in the background and are based on the prioritization for all directive species. The higher the median cell rank is, the higher is its conservation priority. (For interpretation of the references to color in this figure legend, the reader is referred to the online version of this chapter.)

birds directive species includes less overlapping areas with SPAs, and the spatial allocation of N2k is closer to the member state scenario than the EU joint optimum (Table A10). Regarding optimal allocations for habitats and birds directive species, only 38.3% of cells overlap between their EU joint scenarios when looking at the top 18.3% proportion of the landscape (Fig. 5).

When prioritization is done at the level of member states or biogeographical regions, the priorities become more evenly distributed across the EU, but concentrated around borders (Fig. 1, Table A11, Appendix B). For example, in the EU joint scenario, one third of priorities were situated mainly near the external borders of the EU, which represents an edge effect at the scale of the entire region (see Moilanen et al., 2013). N2k grid cells were located on average 53.5 km from the nearest EU member state border, while the average distance to borders from the top 18.3% of cells based on the three administrative scenarios was on average only 41.9 km (Table A12).

4. Discussion

Our study is timely because the European Commission has given a mandate for a “fitness check” on the Birds and Habitats Directives (European Commission, 2015). Here, we quantified the network's potential contribution to the conservation of vertebrate directive species. We compared the N2k to same-sized networks based on hypothetical optimal allocation of sites via spatial prioritization. We found that N2k covers better the distributions of threatened and directive than non-directive vertebrate species, and performs better than a random allocation of sites, as also shown by Gruber et al. (2012). However, in terms of vertebrate species coverage, the N2k is significantly behind the theoretical EU-wide optimal network and closer to optimal allocations developed for smaller administrative units. Thus, as observed also by past studies, a loss in efficiency appears when prioritization is done separately within smaller administrative subunits rather than as a joint community effort (Moilanen et al., 2013; Pouzols et al., 2014).

The goal of the EU has been to secure all species and habitats listed in the two directives. Nevertheless, we found that differences between taxa, both in existing coverage and potential optimal coverage are substantial. While it would be possible to cover very high proportions of the ranges of amphibians and reptiles in an area comparable to the present N2K network, only moderate coverage is possible for mammals and birds in the same area (see also Thuiller et al., 2015). This is due to significantly different mean range sizes (Table A2): small ranges simply are easier to cover than large ones. Here our results support previous research (e.g. Baquero and Telleria, 2001; Maiorano et al., 2013) that found that amphibians and reptiles have overall small ranges and that high rarity and species richness are concentrated in southern Europe. These biogeographical realities should be further accounted for in conservation policies and planning at the EU-level.

When only looking at species' coverage in the N2k, the present coverage levels best correspond to a situation where N2k site selection has followed a national logic based on the interests and constraints of member states (EEA, 2012; Evans, 2012). Nevertheless, in terms of spatial pattern, the N2k is slightly closer to the EU-wide joint priorities for all vertebrate directive species than to optimal allocations done for smaller administrative units, indicating the influence of EU-level policies in the N2k site selection. This is the case for the habitats directive species, while for birds directive species the N2k resembles spatially more an optimal allocation done at the member state level (Table A10). This is in line with the fact that SCI sites for habitats directive species are selected in close cooperation between the EU and the member states, while SPA sites for birds directive species have mostly been selected by member states without application of common EU-wide criteria (Table 1). These are broad patterns, and it is impossible to deduce from the spatial pattern alone the reasons why an individual site has been included in the N2k network.

It has been found previously that global and local conservation priorities do not fully coincide (Moilanen et al., 2013; Pouzols et al., 2014). Our results align with these previous findings (Table A10). We also found that while the EU joint and optimal allocations at lower administrative levels could provide more coverage for vertebrate directive species ranges than the present N2k, the top priority areas would be significantly concentrated near borders between countries, thus forming relatively large contiguous areas (Fig. 1). This edge effect is an outcome of spatial prioritization when arbitrary administrative boundaries (here country borders) subdivide species distributions, thereby causing many species to have their only occurrences inside a country near the border (see Moilanen et al., 2013). Here, the edge effect was visible across all administrative prioritization scenarios. Looking at the present N2K sites, we found that they are on average located significantly further from member state borders than the same extent of top priority areas based on the three administrative optimal allocations (Table A12).

There is another interesting characteristic of spatial prioritization that manifested when a subdivision of biogeographical areas as administrative units was used: the presence of small biogeographical areas that have comparatively many endemic species (Macaronesia) leads to decreased overall efficiency of the solution (Fig. 2). This happens because an equal proportion of protected areas is designated for each administrative unit, meaning that priorities in the area with many endemics become reduced compared to what would be optimal from a broader geographic perspective. Based on present analysis, the biogeographical area approach does not necessarily lead to particularly high continental-level efficiency, at least not if fractional area allocation needs to be equal between sub-regions. However, we found that the biogeographical region scenario covered a relatively large amount of habitats directive species' ranges (Fig. 2). Thus, it seems that many habitats directive species' distributions are more aligned with biogeographical borders rather than member state borders, implying that the selection process of SCIs for habitats directive species, which utilized the biogeographical approach may have been beneficial for habitats directive species.

Our EU joint optimal prioritizations emphasized the role of the southern and northern regions of the EU as concentrations of vertebrate diversity (Fig. 1). Such a theoretical EU-wide optimum is not realistic and politically feasible, because we would need to protect very large areas in the Mediterranean region. Our optimal allocations, which aimed at maximizing species' representations in a complementary manner, are optimums purely in the ecological sense and for vertebrates only. Plants and rare species are known to have driven the selection of some sites (Evans, 2012), which are not likely to be optimal for vertebrates. The N2k also pursues objectives not included in our analysis and it is subject to socio-political and land use constraints that we did not consider either. It would be next too impossible to measure all ecological and socio-political factors that should have influenced site selection across 28 member states and try to find optimized N2k based on these data.

While the optimized N2k (taking into account all ecological and socio-political interests and constraints) remains unattainable, it is important to understand the efficiency loss caused by independent planning for administrative subunits. Here, we quantified this loss by comparing species' coverage in the present N2k to the three hypothetical optimal coverages at different administrative levels. Multiple studies before ours have found that global coordination in conservation delivers greater efficiency than countries acting alone (Kark et al., 2015; Pouzols et al., 2014). However, it is not clear that stakeholders in member states would support an internationally coordinated top-down approach towards conservation, and biodiversity conservation should be also balanced against the preferences that people have in their home countries (Dallimer et al., 2014). Nevertheless, even limited collaboration between countries can lead to improved conservation outcomes via informed compromise between global cost-efficiency and local values.

The N2K has expanded significantly during the past ten years (EEA, 2012). Simultaneously, addition of member states to the EU has resulted in a situation where some member states have large areas (>20% of land) covered by the N2k network while others have lower commitments to the network (Table A1). As additions of new N2k sites have been slowing down, it is unlikely that the N2k would experience significant expansion in the near future. Additionally, it seems that the global trend for example in the implementation of the resolutions of the UN Convention on Biological Diversity is that each country is responsible for their own areas and expands the protected area network approximately to the same 17% coverage of land (CBD, 2016). Equal percentages may be more desirable due to political dynamics.

Especially if N2k expansions will be limited, (say, 1–2% of the EU area), spatial planning tools such as Zonation offer a way forward for identifying areas that increase the representativeness of the network as efficiently as possible. We here found that even small additions could contribute substantially (Fig. 1 panel D; see the steep rise in the orange N2k curve after the 18.3% threshold. In simplified terms, these are the cells outside the N2k that most rapidly increase species representation in the network). While the present policy may not favor site revisions, it may in the future be possible to replace underperforming areas with better alternatives. Additionally, spatial analyses can be used to guide other conservation efforts, such as market-based or voluntary conservation measures (Lehtomäki et al., 2009) that could complement the N2k network. All such analyses should be based on proper data. EU directives include an extensive list of habitats and species from which we only assessed vertebrates due to lack of data about other species groups. Future analyses could be improved by using more up-to-date data and additional data for plants and invertebrates. Including other groups of biodiversity features would lead to a shift in priority areas, as happened here with the inclusion of different taxa (Fig. 5). However, monitoring of sites and assessments on the conservation status and temporal trends of species are crucial. These data should then be used to inform updated studies in species distribution modeling and spatial assessment. Attention could also be given to the improvement of ecological connectivity and the potential of the N2k to provide ecosystem services. Furthermore, since protection outside N2k is required for Annex IV species (Habitats Directive), conservation strategies across entire landscapes should be developed around the N2k. The N2k can be seen as an exceptional and successful community effort in biodiversity conservation. Given the common policy and legislation to protect biodiversity "irrespective of national boundaries", the EU will be an ideal setting for internationally coordinated conservation also in the future.

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Appendix A. Supplementary data

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