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Identifying national responsibility species based on spatial conservation prioritization

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ABSTRACT

The concept of National responsibility species (NRS) was developed to coordinate the conservation efforts of species occurring in multiple countries. Calculated as the fraction of the global species' distribution within a country, it measures the contribution of a local population to global survival of the species. However, there may be more co-occurring species in one region than another, making the conservation of a species more cost-efficient in the first than the latter. If cost-efficient resource allocation is the goal, then identifying NRS should also be based on spatial priorities. We propose that a species is considered NRS when a large part of its distribution falls within high priority areas in a country. We identify NRS from spatial conservation prioritization outputs to (1) maximize the overall cost-efficiency of allocation of conservation resources and (2) to provide information about which species the spatial priorities are based on. We analyzed data on vertebrates in the Birds and Habitats directives in the EU28 countries and compared the traditional NRS measure to three alternative strategies. While the majority of species maintained their NRS status in most countries regardless of the approach, differences occurred, with varying numbers and identities of responsibility species in a country, or responsibilities for species shifting between countries. The differences were largest in geographically marginal countries and for species that were distributed across a few countries. Other NRS approaches may also be useful, and the choice of approach should ultimately depend on the purpose and complement information on conservation status in decision-making.

1. Introduction

Most species are distributed across multiple countries or administrative regions. Because it is not reasonable to expect each country would put equal effort into protection of all species, approaches to identify national responsibility species (hereafter NRS) have been proposed (Schmeller et al., 2008, 2014). Distributing the responsibilities and efforts among countries or other administrative regions in a coordinated manner would enhance the cost-effectiveness of conservation (Pouzols et al., 2014, Kark et al. 2015, Kukkala et al., 2016).

The concept of *responsibility species* has been advocated as complementary to Red Lists for determining conservation priorities, and it represents an estimate of the contribution of the local population to the global survival of the species (Schmeller et al., 2008, Schatz et al., 2014). The ideas on global and regional responsibility derive from the fundamentals in population biology. Population sizes and species diversity strongly vary across geographical areas, and different parts of species' ranges contribute differently to species' survival (Hanski, 1991; Maurer and Taper, 2002). Typical responsibility species approaches are based on the distribution of a species range across countries: a country hosting a large fraction of a species' distribution or total population will have higher responsibility for its protection. This is clear in the case of fully endemic species that cannot be protected elsewhere. For other species, thresholds are usually fixed. In Finland, where national responsibility species have been defined as a part of the Red List assessment, species with 15–20% of the European population in Finland are considered national responsibility species, even though the definition has no legal status (Rassi et al., 2001). These approaches appear to be common in the environmental administration, but have been described in the scientific literature as well (Schnittler and Günther, 1999; Dunn et al., 1999).

Instead of setting a fixed threshold, responsibility can also be determined as a continuous score relative to the area of the country, describing whether the country hosts a larger fraction of the range or population than expected by chance, assuming an even distribution (Keller and Bollmann, 2004). For example, a country that covers 50% of

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the total study area would need to host > 50% of the range of a species to get a score higher than average for the species, while a country that covers 10% of the total area would need to contain over 10% of the range for a similar score (Dunn et al., 1999). Others have proposed that the geographic marginality should also influence responsibility status, so that more weight is given to both central parts of a range as well as to isolated outposts to secure either future refugia, genetic diversity, or evolutionary potential (Schnittler and Günther, 1999). Apart from geographical areas, the concept can also be applied to e.g. a specific habitat type, as was done by Helldin et al. (2015) who defined responsibility species for the Swedish Transport Administration as species that primarily (> 20% of observations) occur on road and railroad verges.

However, if cost-efficiency and cost-effectiveness are taken as guiding principles in conservation planning, especially at an international scale (e.g. EU directive goals), then each species should not be considered in isolation. To make the most of limited resources, international collaboration and coordination of conservation efforts is critical (Naidoo et al., 2006; Moilanen and Arponen, 2011b; Kukkala et al., 2016). While high-resolution georeferenced data on biodiversity have increased, spatial conservation prioritization tools have been developed to aid with the planning process (Kullberg and Moilanen, 2014). These computational tools or software, such as Marxan, (Ball et al., 2009), C-Plan (Pressey et al., 2009) and Zonation (Moilanen et al., 2005) are mainly used for protected area planning, but can be used to spatially target any conservation actions that benefit multiple conservation features (such as species, functions, habitats and ecosystem services) (Pollock et al., 2017).

While complementarity is one of the key approaches to prioritize areas in systematic conservation planning (Margules and Pressey, 2000), the outcomes are often difficult to grasp for conservationists. It is indeed difficult to understand why any individual site was selected as a priority site, as the priorities emerge from the combinations of species occurrences within it and with respect to all the other sites, and often from many additional factors considered in the prioritization. For example, nestedness of species distribution data influences where it is cost-effective to conserve each species (Moilanen and Arponen, 2011a). The picture may be complicated further by additional selection criteria, such as costs (Loyola et al., 2009; Carwardine et al., 2010), connectivity (Cabeza, 2003; Beger et al., 2010; Arponen et al., 2012), threats (Veach et al., 2017) or social and land use constraints (Whitehead et al., 2014; Paloniemi et al., 2018).

Rather than determining responsibilities a priori as input data to spatial prioritization, we propose that national responsibility species could be directly derived from spatial prioritization results. This would (1) ensure that responsibility species are defined in a complementarity-based and cost-efficient manner, and (2) inform decision makers and managers about what spatial priorities are based on, and which species need special attention to maintain the conservation value of the site and thereby of the protected area network as a whole. In our analyses we focus on the European Union and terrestrial vertebrate species distributions in the 28 member states. We identify national responsibility species (NRS) by looking at how Habitats and Birds directive species are distributed within the areas selected as top priorities in different member states. We also look at how species are distributed within the existing Natura 2000 (N2k) network, and identify species whose presence in the network is concentrated to specific countries. We compare alternative NRS approaches to conventional priority species lists derived based on proportion of distribution in each country.

2. Materials & methods

We used results from Kukkala et al. (2016) as the basis for identifying NRS. The purpose of the original analyses was to assess the performance of the N2k network regarding vertebrate species representation with respect to optimal European-wide spatial prioritization with the Zonation software. Here we use the results from the EU-wide analysis to determine national responsibilities: The EU was considered as a joint planning area, and the optimal solution is thus coordinated across all EU countries. An internationally coordinated prioritization is most reasonable as a basis when the purpose is to allocate national responsibilities to individual countries, as it accounts for the total (EU-wide) distribution of each species and prioritizes each where it is most cost-efficient to conserve. Species data and prioritization analysis are described shortly below, but more details can be found in the original publications (data described in Maiorano et al., 2013, analysis described in Kukkala et al., 2016).

2.1. Species data

The data consisted of distribution models for 395 vertebrate species included in the Habitats directive (Annexes II and IV) and Birds directive (Annex I). There were 56 amphibians, 81 reptiles, 77 mammals, and 181 birds included in the analysis representing 90%, 69%, 57% and 93% of the respective directive species (Kukkala et al., 2016). The models were based on extent of occurrence data combined with literature- and expert-based assessments of habitat requirements at 300 m resolution (suitable land cover types, elevation and distance to water). The models were validated against field data. More details can be found in Maiorano et al. (2013). To facilitate computation, the data were aggregated at 1.5 km resolution by summing up the number of suitable 300 m pixels resulting in values ranging from 0 to 25.

2.2. Spatial prioritization

We used spatial prioritization results that are illustrated as a map in Fig. 1A in Kukkala et al. (2016) as our inputs for the present analyses. The prioritization was done with the software Zonation v4.0 (Moilanen et al., 2014). Zonation produces a hierarchical ranking of the full landscape based on species' occurrences (raster maps). It iteratively removes cells one by one minimizing the marginal loss of conservation value. We used the core-area cell removal rule in the algorithm, which aims at maintaining high-quality areas for all species among the prioritized sites. The marginal loss (δ_i) for cell i is calculated as:

$$\delta_i = \max_j \frac{Q_{ij}(S)w_j}{c_i}$$

where j are species with weights of w, and c indicates the costs for the cells. $Q_{ij}(S)$ is the proportion of range for species j in cell i out of the range in all remaining cells (S). In practice, the algorithm removes first the cells that contain species that are broadly distributed in the landscape, and retains last the core areas of species distributions. The CAZ objective coincides well with the N2k target of retaining the best habitats and preserving all directive species, as opposed to the alternative Zonation approach where larger trade-offs among species' representation are allowed (Additive Benefit Function). The core-area variant is also well suited for identifying national responsibilities: The idea of defining national responsibility species based on range size considerations is based on the premise that all species should be protected, even if some species are more costly to cover than others. In our analysis cost data and species weights were not used (costs and weights were assigned as 1 for all cells and species), and the proportions of suitable habitat in cell (values from 0 to 25 as described above) were used to calculate $Q_{ij}(S)$.

2.3. Determining national responsibilities

A simplified process flow chart of how the different NRS lists were created is given in Fig. 1. We used species distribution maps, data on country borders, N2k area, and an output map from the EU-wide spatial prioritization by Kukkala et al. (2016) The priority map contains unique

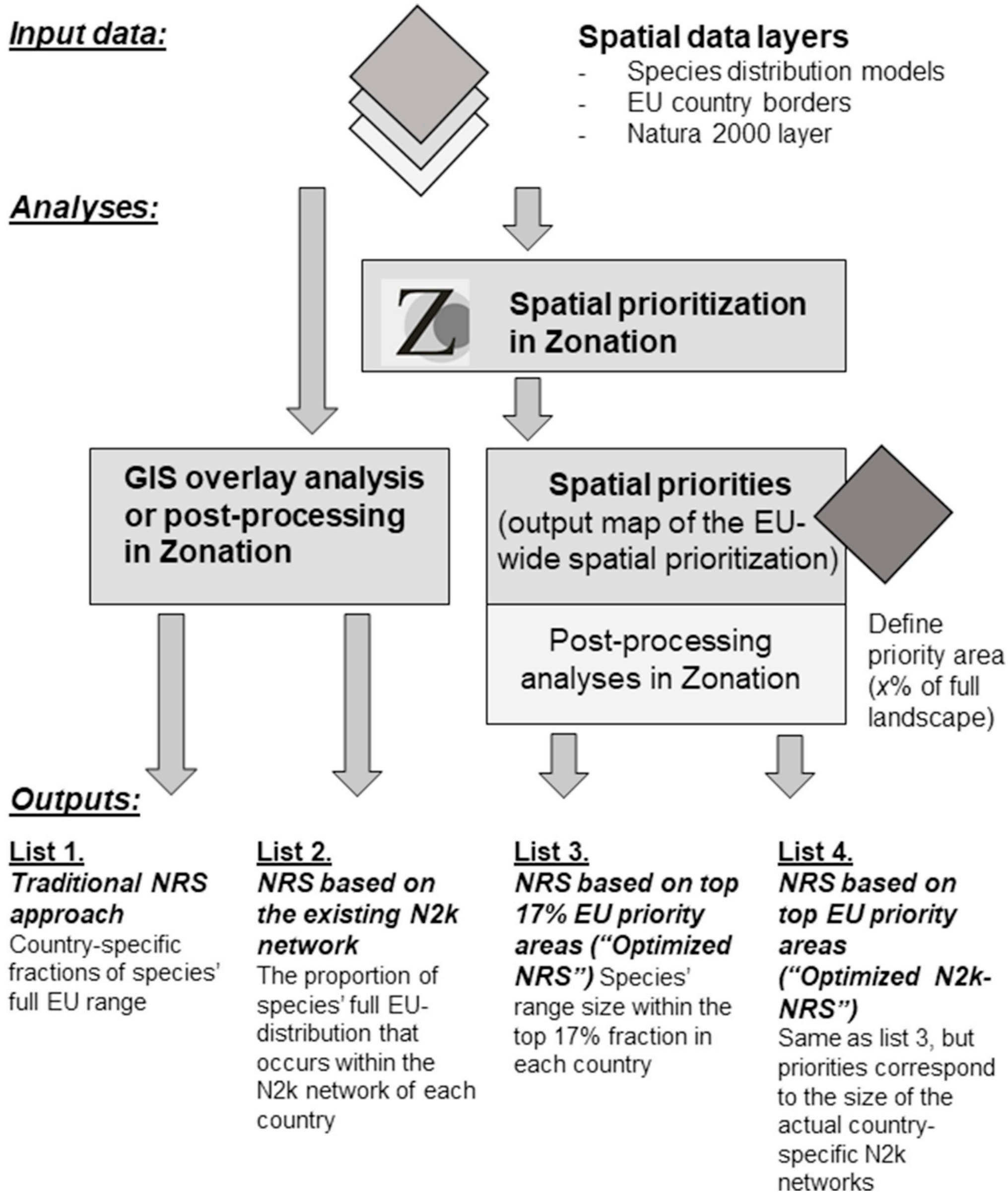
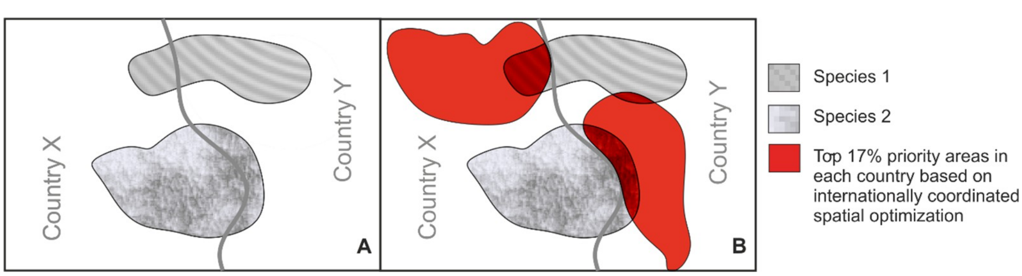


Fig. 1. A simplified process flow chart of how the four different NRS lists were created.



NRS approach	Country X	Country Y
A) Traditional NRS: Fraction of species full range within country (List 1)	Sp 1 (22%) Sp 2 (70%)	Sp 1 (78%) Sp 2 (30%)
B) Optimized NRS: Fraction of species range within top priority areas (List 3)	Sp 1 (20%)	Sp 2 (18%) Sp 1 (3%)

Fig. 2. A simplified figure example and a table illustrating the differences between two of the responsibility species approaches. A) shows the traditional approach determined by fraction of range within each country (List 1). B) shows how species ranges overlap with priority areas (red), and only the fraction overlapping with those areas is considered within each country out of total range size (List 3). In our analyses the red areas would represent the top 17% priority areas identified by spatial prioritization. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rank values from 0 (least valuable) to 1 (most valuable) for each raster cell. These can be used to extract an area corresponding to any top fraction of the landscape. We conducted post-processing analyses in Zonation (see below and Appendix 1), and produced four different NRS descriptions and lists of species. The first two were based on species distributions overlaid with country borders (list 1) or N2k raster (list 2). The latter two (3–4) were based on spatial prioritization results (the optimized solution for the whole EU by Kukkala et al. (2016)). The differences between these are illustrated in Fig. 2. Rather than setting some pre-determined area coverage threshold to define national responsibility, in each approach we rank the species in decreasing order of national responsibility (rank values ranging from 100 to 0%).

1) *Traditional NRS approach – country-specific fraction of full EU range ("Traditional NRS").* Responsibility species based on range distributions in the countries (x% of the full EU-distribution), corresponding to the traditional approach, except that we provide a list of species in decreasing order of range within country instead of using a threshold value for selecting species.
2) *NRS based on the existing N2k network ("N2k NRS")*. We listed the species in decreasing order of the proportion of full EU-distribution that occurs within the N2k network of each country. In other words, species that have small ranges in the EU but are well represented in the N2k of a country rank highest. This alternative allows comparing the actual N2k achievement to optimal allocation of equal effort (list 4). Note that the actual size of the N2k networks vary in different countries.
3) *NRS based on top 17% EU priority areas ("Optimized NRS").* Responsibility species based on EU-wide prioritization by Zonation, considering an equal top fraction of the priorities in each country, 17%, corresponding to the Aichi target 11 (Convention on Biological Diversity, 2010). For each country we listed the species in decreasing order of range size within the top 17% fraction.
4) *NRS based on top EU priority areas, corresponding to the size of actual country-specific N2k ("Optimized N2k-NRS").* Responsibility species based on EU-wide prioritization, and assuming each country would protect the same percentage of area they actually had in their national N2k networks (ranging between 10% and 38% of area). Countries would now start their N2k networks from scratch and protect the areas proposed by our EU-wide spatial prioritization. We listed the species in decreasing order of range size within the top fraction.

Technically, all the NRS lists were obtained by post-processing steps in Zonation software. Similar lists could be produced with operations in any GIS software by overlaying species distribution maps with country borders (list 1) or existing protected areas (list 2). In addition, we overlayed species distribution maps with areas of the 17% priorities (optimal solution for the whole EU) produced by the Zonation prioritization software (producing lists 3–4). Effectively, Zonation calculates statistics about each biodiversity feature across pre-determined areas (e.g. countries and country-specific N2k's) via so called LSM analysis (Landscape identification for masked subregion of landscape). Detailed information on the post-processing analyses can be found from Zonation manual (Moilanen et al., 2014, page 138) and on our post-processing analyses from Appendix 1.

3. Results

Full species lists of all five NRS alternatives for all countries can be found in the first sheet of Appendix 2. To facilitate comparisons among the lists, we have highlighted in yellow the same total number of top-ranked species in the different lists (list 4 has one species more due to a tie in rank). In the traditional NRS approach (list 1) we highlighted all species that had at least 17% of their distribution within a country, which resulted in 571 responsibility species across 23 European countries, leaving 5 countries without any responsibility species (Table 1, Appendix 2). For ease of comparison, we then highlighted the same number of top-ranked species in the other NRS lists, resulting in redistributed numbers of alternative responsibility species in the countries. We chose to redistribute the same number of species based on rank order because the numeric values in the different approaches are

Table 1
Numbers of responsibility species in each country with the five different NRS approaches.

Country	N2k coverage %	Number of spp	Endemics	(1) Trad. NRS	(2) N2k NRS	(3) Optimized NRS	(4) Optimized N2k-NRS
Austria	15.1	147	0	5	4	4	4
Belgium	12.8	96	0	0	0	0	0
Bulgaria	34.2	186	0	28	41	37	54
Cyprus	17.1	52	3	8	5	13	13
Czech_Republic	14.0	133	0	0	0	0	0
Germany	16.1	146	0	9	7	2	2
Denmark	12.3	83	0	0	0	0	0
Spain	27.3	208	30	116	118	120	129
Estonia	19.6	103	0	3	6	5	4
Finland	14.4	100	1	53	38	38	29
France	13.1	195	3	60	40	39	38
United_Kingdom	9.8	91	2	11	8	11	10
Greece	26.9	205	14	60	64	81	85
Croatia	37.2	173	0	7	17	17	20
Hungary	21.4	144	0	6	7	7	7
Ireland	15.5	48	0	2	5	6	5
Italy	19.4	206	15	63	68	75	68
Lithuania	12.6	117	0	1	1	1	1
Luxembourg	17.9	66	0	0	0	0	0
Latvia	11.9	111	0	2	3	4	1
Malta	19.9	18	1	2	1	2	2
Netherlands	12.9	96	0	0	0	2	1
Poland	19.7	150	2	15	20	7	6
Portugal	20.9	138	6	20	26	28	26
Romania	22.5	184	0	42	52	40	39
Sweden	12.9	119	0	54	34	26	17
Slovakia	29.7	143	0	2	3	2	3
Slovenia	37.7	147	0	2	3	4	7

not comparable: The fractions of full distributions are necessarily much lower than fractions of prioritized distributions. The numbers of top-ranked species with each approach in each country are given in Table 1.

When there are many endemic and near-endemic species, the approaches differ very little (e.g. in Spain). Similarly, at the other end of the spectrum, when no species have a significant proportion of their range inside the country, be that over the entire country or its priority sites, none of the approaches will consider the species as responsibility for the country. This will happen mainly with small, continental countries such as Denmark or Belgium.

Similarly, species that are distributed across many countries are unlikely to be of high priority in any, while endemic species are necessarily the responsibility of their host. Most variation is seen with species that are in between the two extremes, occurring over a handful of countries: They have substantial parts of their distribution in more than one country, among which the priorities may shift depending on approach.

Even when no species are considered as national responsibility based on some cut-off value, the lists can nevertheless be inspected country-wise to assess which species have highest priority within the country. This provides useful information at the national level that is independent of the influence of the country's size on the number of responsibility species. For example, even though it has no NRS according to our classification, the Czech Republic sustains 10% of the total EU range of the European fire-bellied toad (*Bombina bombina*) and 8% of range of the European hamster (*Cricetus cricetus*), which are the first two species on the Traditional NRS list for the country. The former ranks consistently high with all approaches, whereas the latter drops dramatically in the other lists, indicating that the range of the hamster in the country does not align well with spatial priorities, nor with existing N2k sites (Appendix 2). Alternatively, the lists can also be ranked species-wise to see which countries have the highest responsibility for any given species (Appendix 2, sheets 2–5).

We selected a few example countries with different biogeographical characteristics for closer examination. The alternative shortlists for top ranking species in them are given in Table 2.

Cyprus is an example where numbers of responsibility species vary between approaches, while the species on each are largely the same and vary only in order. It is a small country, but being an island, it has three endemic species and a few others that have a significant proportion of their range in the country. It is a location where conservation would be cost-efficient for many more species, resulting in a larger number of responsibility species with Optimized NRS approach (list 3). It's existing N2k network (N2k NRS, list 2) does not hold nearly similar proportions of those species' ranges as would be theoretically possible with optimally located corresponding area (Optimized N2k-NRS, list 4).

Finland on the other hand has a relatively large land area. As a northern country, it does not hold a great diversity considering its size, but being located at a geographical extreme of the European Union, it has many species with marginal ranges to the EU, and consequently, many responsibility species based on range size only (Traditional NRS, list 1). Number of responsibility species drops when cost-efficient allocation is considered (Optimized NRS and Optimized NN2k-NRS, lists 3–4), as conservation of many of its species might be more cost-efficient elsewhere (covering more species as a by-product).

Even endemic or near-endemic species can rank differently within their host country's species lists depending on range size within the country. For example, the Siberian flying squirrel (*Pteromys volans*), despite having a broad range globally, has > 96% of its EU-range within Finland, making it the second highest ranking species in the country when responsibilities are based on fractions of range in the country (Traditional NRS, list 1, Appendix 2 and Table 2). However, being rather broadly distributed within Finland, existing protected areas or hypothetical priority sites cannot cover a large fraction of its distribution, and it drops in rank below many other species that have narrower overall distributions (Optimized NRS and Optimized N2k-NRS, lists 3–4). Its particularly poor representation in N2k (N2k NRS, list 2) is probably mainly due to it being a southern species, whereas protected areas are strongly concentrated in the northern parts of the country.

Other species may instead change country of responsibility depending on approach. For example the Italian crested newt (*Triturus carnifex*), having 20% of its range in Austria ranks as the 4th out of five responsibility species when considering fraction of range within country (Traditional NRS, list 1), but drops out of the lists with the other approaches. It has 58% of its range in Italy, and there it tends to maintain its position in mid-ranking responsibility species. It is among the better represented species in the Italian N2k, when measured as proportion of range in the network (N2k NRS, list 2).

4. Discussion

We introduced new, alternative approaches to identifying NRS that account for cost-efficiency of conservation, and applied them to data on vertebrates in the Birds and Habitats directives in the EU28 countries. Some of the countries and species showed notable differences between the alternative approaches to defining national responsibility species: The numbers and identities of responsibility species in a country may vary, or responsibilities for species may shift from one country to another. Issues influencing whether or not changes take place include, but are not limited to, the number of countries a species occurs in, the geographical location and the degree of endemism in the country, and the overall species richness in the country. But as the spatial prioritization process is complex and depends on the structure of the entire dataset as well as analysis options chosen, it is impossible to predict the outcome based on data characteristics only. Spatial prioritization and defining responsibilities based on the results is the only way to account for cost-efficiency in the process.

We used the Zonation software for prioritization, but it should be noted that the proposed NRS alternatives are not tied to any specific prioritization tool. What is required are maps indicating the spatial priorities, which can be produced with any spatial prioritization software such as Marxan (Ball et al., 2009) or C-plan (Pressey et al., 2009), and data on species distributions that can be overlaid with the spatial priorities. Clearly, the choice of method and data used should be determined by what is desired from the NRS. Indeed, an advantage (and potential complication) of identifying responsibility species based on spatial conservation prioritization is that it is possible to account for many kinds of additional factors. In addition to obvious choices, such as which taxa are included, a whole range of factors could have an impact on spatial priorities and thereby on NRS: Habitat quality, threats, conservation status, various kinds of costs, the geographical position within the range accounting for future range shifts, socio-political constraints etc. (Carwardine et al., 2010, Kullberg and Moilanen, 2014, Veach et al., 2017, Paloniemi et al., 2018). Considering factors that influence *the likelihood of conservation success* helps with assigning responsibilities to locations where the species are most likely to survive with least cost. Inclusion of such factors to NRS identification would help with achieving cost-effectiveness, instead of mere cost-efficiency.

Also factors such as genetic diversity, phylogenetic diversity (PD) and functional diversity (FD) can be considered in the prioritization (Taberlet et al., 2012; Arponen and Zupan, 2016; Pollock et al., 2017), and hence influence the co-benefits and the national responsibilities as well. Certain populations may contain disproportionate amounts of the genetic diversity within the species, and if data are available, they can be accounted for in the prioritization. We may also want to prioritize sites with high FD as a proxy for ecosystem function, and consequently, a species may be primarily protected in a region with high FD even though it occurred elsewhere as well (Thuiller et al., 2015). Alternatively, we may want to give more importance to species that contribute more to the total PD and represent larger fractions of evolutionary history than average (Pollock et al., 2017). Such weightings and

Table 2
Species lists for four example countries. NRS rank values are given here as percentage values from 0 to 100%, indicating the percentage of distribution considered in each NRS alternative (e.g. from List 1 you can see that 57% of the full distribution of *Salamandra atra* occurs in Austria).

	List (1) "Traditional NRS"	NRS rank	List (2) "N2k NRS"	NRS rank	List (3) "Optimized NRS"	NRS rank	List (4) "Optimized N2k-NRS"	NRS rank
Austria	*Salamandra atra*	57	*Marmota marmota*	9	*Salamandra atra*	22	*Salamandra atra*	17
	Marmota marmota	29	*Rupicapra rupicapra*	8	*Marmota marmota*	16	*Marmota marmota*	14
	Rupicapra rupicapra	24	*Salamandra atra*	7	*Rupicapra rupicapra*	14	*Rupicapra rupicapra*	12
	Triturus carnifex	20	*Alectoris graeca*	5	*Alectoris graeca*	9	*Alectoris graeca*	8
	Iberolacerta horvathi	20						
Cyprus	*Dolichophis cypriensis*	100	*Dolichophis cypriensis*	37	*Dolichophis cypriensis*	100	*Dolichophis cypriensis*	100
	Oenanthe cypriaca	100	*Sylvia melanothorax*	13	*Sylvia melanothorax*	99	*Sylvia melanothorax*	99
	Sylvia melanothorax	100	*Oenanthe cypriaca*	11	*Oenanthe cypriaca*	99	*Oenanthe cypriaca*	98
	Hemorrhois nummifer	90	*Hemorrhois nummifer*	11	*Hemorrhois nummifer*	89	*Hemorrhois nummifer*	89
	Hoplopterus spinosus	37	*Hoplopterus spinosus*	5	*Hoplopterus spinosus*	37	*Hoplopterus spinosus*	37
	Ovis aries	32			*Ovis aries*	32	*Ovis aries*	31
	Laudakia stellio	29			*Laudakia stellio*	28	*Laudakia stellio*	28
	Ophisops elegans	22			*Ophisops elegans*	22	*Ophisops elegans*	22
					Plecotus kolombatovici	14	*Plecotus kolombatovici*	14
					Chamaeleo chamaeleon	11	*Chamaeleo chamaeleon*	11
					Chalcides ocellatus	11	*Chalcides ocellatus*	11
					Emberiza caesia	9	*Emberiza caesia*	9
					Lanius nubicus	7	*Lanius nubicus*	7
Finland	*Rangifer tarandus*	100	*Limosa lapponica*	55	*Rangifer tarandus*	90	*Rangifer tarandus*	82
	Pteromys volans	96	*Anser erythropus*	27	*Xenus cinereus*	66	*Xenus cinereus*	66
	Larus minutus	78	*Alopex lagopus*	26	*Limosa lapponica*	51	*Limosa lapponica*	41
	Limosa lapponica	74	*Nyctea scandiaca*	26	*Sterna caspia*	38	*Sterna caspia*	35
	Mergus albellus	73	*Charadrius morinellus*	19	*Aquila clanga*	33	*Aquila clanga*	33
	Gulo gulo	69	*Falco rusticolus*	19	*Larus minutus*	28	*Anser erythropus*	24
	Xenus cinereus	67	*Sterna paradisaea*	17	*Anser erythropus*	27	*Alopex lagopus*	21
	Cygnus cygnus	59	*Calidris alpina*	16	*Alopex lagopus*	25	*Nyctea scandiaca*	21
	Strix nebulosa	57	*Lagopus mutus*	16	*Nyctea scandiaca*	25	*Microtus oeconomus*	20
	Gavia stellata	56	*Larus minutus*	14	*Microtus oeconomus*	24	*Larus minutus*	19
	Podiceps auritus	54	*Microtus oeconomus*	14	*Sterna paradisaea*	23	*Sterna paradisaea*	19
	Surnia ulula	51	*Phalaropus lobatus*	14	*Phalaropus lobatus*	22	*Phalaropus lobatus*	17
	Sterna caspia	51	*Cygnus cygnus*	13	*Pteromys volans*	21	*Pteromys volans*	16
	Phalaropus lobatus	51	*Gavia stellata*	13	*Cygnus cygnus*	21	*Falco rusticolus*	16
	Sterna paradisaea	43	*Mergus albellus*	13	*Gavia stellata*	20	*Branta leucopsis*	16
	Gavia arctica	42	*Gulo gulo*	12	*Podiceps auritus*	19	*Cygnus cygnus*	15
	Microtus oeconomus	40	*Gavia arctica*	10	*Falco rusticolus*	19	*Gavia stellata*	15
	Ursus arctos	39	*Aquila clanga*	10	*Mergus albellus*	18	*Sterna hirundo*	14
	Tringa glareola	39	*Philomachus pugnax*	10	*Charadrius morinellus*	17	*Calidris alpina*	14
	Picoides tridactylus	37	*Podiceps auritus*	8	*Sterna hirundo*	17	*Uria aalge*	14
	Tetrao tetrix	36	*Pluvialis apricaria*	8	*Calidris alpina*	17	*Charadrius morinellus*	14
	Porzana porzana	35	*Falco columbarius*	8	*Chlidonias niger*	17	*Chlidonias niger*	14
	Sicista betulina	35	*Sterna hirundo*	8	*Branta leucopsis*	17	*Podiceps auritus*	14
	Pandion haliaetus	35	*Grus grus*	7	*Gavia arctica*	15	*Mergus albellus*	13
	Strix uralensis	33	*Xenus cinereus*	7	*Lagopus mutus*	14	*Lagopus mutus*	11
	Aquila clanga	33	*Sterna caspia*	7	*Uria aalge*	14	*Gavia arctica*	11
	Sterna hirundo	32	*Tringa glareola*	6	*Gulo gulo*	13	*Gulo gulo*	10
	Anser erythropus	32	*Strix nebulosa*	6	*Grus grus*	12	*Grus grus*	10
	Circus aeruginosus	32	*Surnia ulula*	6	*Philomachus pugnax*	11	*Philomachus pugnax*	9
	Calidris alpina	31	*Luscinia svecica*	6	*Circus aeruginosus*	10		
	Grus grus	30	*Picoides tridactylus*	6	*Porzana porzana*	9		
	Alopex lagopus	30	*Chlidonias niger*	5	*Tringa glareola*	9		
	Nyctea scandiaca	29	*Pandion haliaetus*	5	*Strix nebulosa*	9		
	Chlidonias niger	29	*Ursus arctos*	5	*Pluvialis apricaria*	8		
	Aegolius funereus	29	*Circus aeruginosus*	5	*Falco columbarius*	8		
	Philomachus pugnax	28	*Aquila chrysaetos*	5	*Pandion haliaetus*	8		
	Canis lupus	28	*Asio flammeus*	5	*Ursus arctos*	7		
	Glaucidium passerinum	27	*Rangifer tarandus*	4	*Surnia ulula*	7		
	Luscinia svecica	27			*Luscinia svecica*	5		
	Tetrao urogallus	27						
	Botaurus stellaris	26						
	Charadrius morinellus	26						
	Lynx lynx	25						
	Ficedula parva	25						
	Bonasa bonasia	25						
	Rana arvalis	24						
	`*Falco columbarius*	24						
	Pluvialis apricaria	23						
	Falco rusticolus	22						
	Lagopus mutus	21						
	Eptesicus nilsonii	21						
	Dryocopus martius	18						
	``*Branta leucopsis*	18						
	Myotis daubentonii	17						

(*continued on next page*)

Table 2 (*continued*)

	List (1) "Traditional NRS"	NRS rank	List (2) "N2k NRS"	NRS rank	List (3) "Optimized NRS"	NRS rank	List (4) "Optimized N2k-NRS"	NRS rank
Italy	*Rana italica*	100	*Atylodes genei*	48	*Euproctus platycephalus*	100	*Euproctus platycephalus*	100
	Atylodes genei	100	*Speleomantes supramontis*	47	*Speleomantes flavus*	100	*Speleomantes flavus*	100
	Bombina pachypus	100	*Euproctus platycephalus*	42	*Speleomantes supramontis*	100	*Speleomantes supramontis*	100
	`Euproctus platycephalus	100	*Lissotriton italicus*	39	*Emys trinacris*	100	*Emys trinacris*	100
	Lissotriton italicus	100	*Discoglossus pictus*	37	*Discoglossus pictus*	100	*Discoglossus pictus*	100
	Pseudepidalea sicula	100	*Salamandrina terdigitata*	36	*Speleomantes imperialis*	100	*Speleomantes imperialis*	100
	Salamandrina perspicillata	100	*Bombina pachypus*	33	*Plecotus sardus*	100	*Speleomantes ambrosii*	100
	Salamandrina terdigitata	100	*Rana italica*	33	*Atylodes genei*	100	*Atylodes genei*	100
	Speleomantes ambrosii	100	*Salamandrina perspicillata*	29	*Speleomantes ambrosii*	100	*Plecotus sardus*	100
	Speleomantes flavus	100	*Hyla intermedia*	28	*Pseudepidalea sicula*	98	*Pseudepidalea sicula*	99
	Speleomantes imperialis	100	*Speleomantes imperialis*	27	*Podarcis wagleriana*	96	*Podarcis wagleriana*	97
	Speleomantes supramontis	100	*Plecotus sardus*	25	*Crocidura sicula*	95	*Crocidura sicula*	96
	Hystrix cristata	100	*Emys trinacris*	23	*Salamandrina terdigitata*	92	*Salamandrina terdigitata*	93
	Plecotus sardus	100	*Archaeolacerta bedriagae*	20	*Lissotriton italicus*	83	*Lissotriton italicus*	85
	Emys trinacris	100	*Zamenis lineatus*	18	*Speleomantes strinatii*	83	*Speleomantes strinatii*	84
	Podarcis wagleriana	100	*Salamandra lanzai*	17	*Bombina pachypus*	78	*Bombina pachypus*	80
	Zamenis lineatus	100	*Rupicapra rupicapra*	17	*Rana italica*	78	*Rana italica*	80
	Discoglossus pictus	100	*Speleomantes strinatii*	17	*Archaeolacerta bedriagae*	78	*Rana latastei*	79
	Crocidura sicula	100	*Triturus carnifex*	16	*Algyroides fitzingeri*	77	*Algyroides fitzingeri*	78
	Hyla intermedia	98	*Marmota marmota*	16	*Podarcis tiliguerta*	76	*Archaeolacerta bedriagae*	78
	Podarcis sicula	94	*Algyroides fitzingeri*	16	*Rana latastei*	75	*Podarcis tiliguerta*	77
	Pseudepidalea balearica	92	*Alectoris graeca*	16	*Salamandrina perspicillata*	73	*Salamandrina perspicillata*	75
	Rana latastei	90	*Myotis punicus*	16	*Alectoris barbara*	69	*Alectoris barbara*	70
	Speleomantes strinatii	88	*Larus audouinii*	16	*Sylvia sarda*	63	*Sylvia sarda*	64
	Podarcis tiliguerta	85	*Hystrix cristata*	16	*Myotis punicus*	60	*Hyla intermedia*	60
	Algyroides fitzingeri	83	*Podarcis wagleriana*	15	*Salamandra lanzai*	59	*Myotis punicus*	60
	Archaeolacerta bedriagae	78	*Hyla sarda*	15	*Hyla intermedia*	58	*Salamandra lanzai*	59
	Alectoris barbara	77	*Discoglossus sardus*	15	*Zamenis lineatus*	55	*Zamenis lineatus*	57
	Sylvia sarda	68	*Speleomantes ambrosii*	15	*Euleptes europaea*	54	*Euleptes europaea*	54
	Falco biarmicus	62	*Pseudepidalea sicula*	15	*Ovis aries*	51	*Ovis aries*	52
	Myotis punicus	60	*Podarcis tiliguerta*	14	*Discoglossus sardus*	49	*Discoglossus sardus*	49
	Elaphe quatuorlineata	60	*Pseudepidalea balearica*	14	*Hyla sarda*	49	*Hyla sarda*	49
	Salamandra lanzai	59	*Podarcis sicula*	13	*Chalcides ocellatus*	40	*Chalcides ocellatus*	40
	Triturus carnifex	58	*Speleomantes flavus*	13	*Hystrix cristata*	37	*Hystrix cristata*	39
	Euleptes europaea	57	*Crocidura sicula*	13	*Triturus carnifex*	36	*Triturus carnifex*	38
	Ovis aries	55	*Sylvia sarda*	13	*Pseudepidalea balearica*	36	*Pseudepidalea balearica*	37
	Discoglossus sardus	50	*Larus genei*	13	*Podarcis sicula*	35	*Podarcis sicula*	36
	`Hyla sarda	49	*Vipera ursinii*	13	*Larus audouinii*	30	*Larus audouinii*	30
	Hierophis viridiflavus	44	*Alectoris barbara*	12	*Larus genei*	22	*Myotis capaccinii*	22
	Chalcides ocellatus	42	*Puffinus yelkouan*	12	*Myotis capaccinii*	22	*Larus genei*	22
	Lacerta bilineata	36	*Myotis capaccinii*	12	*Marmota marmota*	21	*Marmota marmota*	22
	Marmota marmota	35	*Rana latastei*	12	*Vipera ursinii*	21	*Rupicapra rupicapra*	21
	Rupicapra rupicapra	34	*Euleptes europaea*	12	*Rupicapra rupicapra*	20	*Vipera ursinii*	21
	Alectoris graeca	32	*Porphyrio porphyrio*	11	*Puffinus yelkouan*	20	*Puffinus yelkouan*	20
	Larus audouinii	30	*Elaphe quatuorlineata*	11	*Porphyrio porphyrio*	19	*Falco biarmicus*	19
	Natrix tessellata	28	*Ovis aries*	10	*Falco biarmicus*	18	*Porphyrio porphyrio*	19
	Salamandra atra	27	*Falco biarmicus*	10	*Alectoris graeca*	17	*Alectoris graeca*	18
	Tadarida teniotis	27	*Phoenicopterus roseus*	10	*Hierophis viridiflavus*	16	*Hierophis viridiflavus*	17
	Plecotus macrobullaris	26	*Calonectris diomedea*	9	*Elaphe quatuorlineata*	15	*Elaphe quatuorlineata*	16
	Myotis capaccinii	25	*Salamandra atra*	8	*Calonectris diomedea*	14	*Calonectris diomedea*	15
	Pipistrellus savii	23	*Podarcis filfolensis*	8	*Charadrius alexandrinus*	14	*Charadrius alexandrines*	14
	Vipera ursinii	23	*Chalcides ocellatus*	8	*Falco eleonorae*	14	*Falco eleonorae*	14
	Larus genei	22	*Hierophis viridiflavus*	6	*Pipistrellus savii*	13	*Pipistrellus savii*	13
	Rhinolophus euryale	22	*Pipistrellus savii*	6	*Rana dalmatina*	12	*Rana dalmatina*	12
	Miniopterus schreibersi	21	*Natrix tessellata*	6	*Testudo hermanni*	12	*Testudo hermanni*	12
	Puffinus yelkouan	20	*Charadrius alexandrinus*	6	*Tadarida teniotis*	10	*Tadarida teniotis*	11
	Lanius minor	20	*Falco eleonorae*	6	*Salamandra atra*	10	*Salamandra atra*	11
	Porphyrio porphyrio	19	*Plecotus macrobullaris*	6	*Phoenicopterus roseus*	10	*Lacerta bilineata*	10
	Testudo hermanni	19	*Hydrobates pelagicus*	5	*Lacerta bilineata*	10	*Natrix tessellata*	10
	Rana dalmatina	18	*Lacerta bilineata*	5	*Natrix tessellata*	10	*Phoenicopterus roseus*	10
	Calandrella brachydactyla	18	*Rana dalmatina*	5	*Podarcis filfolensis*	10	*Rhinolophus euryale*	10
	Pipistrellus kuhlii	18	*Tadarida teniotis*	5	*Rhinolophus euryale*	9	*Podarcis filfolensis*	10
	Melanocorypha calandra	18	*Rupicapra pyrenaica*	5	*Plecotus macrobullaris*	9	*Plecotus macrobullaris*	9
			Sterna albifrons	5	*Rhinolophus mehelyi*	8	*Melanocorypha calandra*	9
			Aythya nyroca	5	*Melanocorypha calandra*	8	*Rhinolophus mehelyi*	8
			Recurvirostra avosetta	4	*Hydrobates pelagicus*	8	*Rhinolophus ferrumequinum*	8
			Acrocephalus melanopogon	4	*Rhinolophus ferrumequinum*	8	*Hydrobates pelagicus*	8
			Testudo hermanni	4	*Sterna albifrons*	7	*Sterna albifrons*	7
					Calandrella brachydactyla	7	*Calandrella brachydactyla*	7
					Hyla meridionalis	7		
					Zamenis situla	7		
					Ardeola ralloides	7		
					Pipistrellus kuhlii	7		
					Recurvirostra avosetta	7		
					Plegadis falcinellus	7		

considerations in the prioritization will drive the solution toward certain areas, which in turn will influence which species become of national responsibility in each country. Therefore, for transparency, it is always good to first prioritize without any weightings and compare the solutions.

Our spatial prioritization was based on maximizing cost-efficiency across the EU, which necessarily results in and uneven distribution of conservation effort among the countries. Equity among countries and cost-efficiency can be traded off against each other in the prioritization in Zonation (Moilanen and Arponen, 2011b), resulting in a balanced distribution of conservation effort and thereby affecting the identities of the NRS. In addition, in our approach there is no need to set arbitrary threshold values (targets) for responsibility beforehand (e.g. a certain percentage of species coverage needed), which would result in highly uneven numbers of species among the countries. Instead, we recommend looking at the species lists in decreasing order until reaching a percentage level or number of species suitable for the country and purpose in question. In other words, the lists identify the most important (highest responsibility) species for each country regardless of how they compare to other countries and what the exact numeric values are.

In the approach we used in our example only species with narrow ranges can rank high in the list of any one country (e.g. 17% of the landscape cannot contain a large fraction of a large range). If the goal is to assign a responsibility country for each species, then the results can equally well be ranked by species rather than by country, and see which countries contain largest fractions of the species' range.

The flexibility of our approach allows for changing the reference for calculating the proportions of distribution from the full distribution to e.g. the part of a range that falls inside the protected area network. This option would follow the precautionary principle, assuming unprotected areas cannot guarantee species persistence. Here species would be the responsibility of countries whose protected areas hold largest part of the species distribution within the whole international network. In other words, it would coordinate responsibilities inside the protected area network.

While our method is highly flexible and applicable to many situations, it should be noted that it is a technical tool built to support decision making, and should not be applied without expert knowledge and post hoc assessment of the outcomes. Especially when applied at a continental scale, international coordination is required to ensure responsibilities are reasonably distributed, while keeping in line with the international conservation objectives. In the case of the EU, responsibilities could be centrally coordinated to ensure protection of all of the Directive species, just as with the establishment of the Natura 2000 network, and to alleviate the burden of the most diverse countries by e.g. limiting the number of NRS and reallocating some species to other, less diverse countries.

Spatial prioritization is used typically, although not exclusively, on protected area planning (Moilanen et al., 2009). One might argue that identifying NRS could be redundant as the prioritized areas are protected with all the species in them. But it is relevant for allocating further conservation efforts, e.g. threat management, restoration efforts, legal protection and all other actions helping with the maintenance of population viability both within the protected areas as well as at broader scales, if the species occurs also outside the protected areas. Apart from national priorities, the approach presented here is applicable at any spatial or administrative scale and extends even to the level of a single protected area: Prioritization outputs can be explored to understand which species have contributed most to the fact that the site has been prioritized. If the justification for the establishment of a protected area is that responsibility species occur there (as often with N2K for directive species), then it should be made especially certain that those species will persist. Concepts such as irreplaceability (Pressey et al., 1994; Ferrier et al., 2000) and replacement-cost (Cabeza and Moilanen, 2006) only indicate the value of the site as a component of the prioritized network and not what it's based on and how to maintain it best.

One should also acknowledge that NRS is a relative measure, indicating which country should bear more responsibility with respect to the others. We did not consider threat status, range size in absolute terms, or wintering ranges for migratory birds. Our data consisted of the EU Directive species, meaning that their conservation has been prioritized in the EU by legislation (the Birds Directive 79/409/EEC and the Habitats Directive 92/43/EEC), and we did not attempt to assess whether prioritizing their conservation in the EU makes sense in the first place. Many of the Directive species have broad distributions outside the EU, but assessing responsibilities in the global scale is beyond the scope of this paper. Endangered species, instead, sometimes with very restricted distribution ranges, would typically always have high priority everywhere regardless of the proportion of range in any specific place (unless a strict triage approach is adopted, e.g. McDonald-Madden et al., 2008). NRS lists should complement rather than replace information on conservation status in decision-making. Importantly, NRS could guide proactive actions on the less threatened species.

Range-size considerations may be important for conservation, but do not necessarily indicate conservation needs of the species, and clearly those must be independently considered in decision-making. It also depends on the context, whether the characteristics of the proposed approach are desirable to begin with: In addition to helping with allocating targeted conservation actions, responsibility can also imply, for instance, that the country that hosts a large part of the global population should keep track of population trends more closely, in which case population size per country is the relevant measure.

NRS can also have various roles independent of cost-efficiency, in which case characteristics of the traditional range-based NRS definitions may be more suitable. For instance, human-nature connectedness manifests at different spatial scales and may be mediated by factors such as place-attachment or patriotism, influencing pro-environmental behavior (Dallimer et al., 2015, Klaniecki et al., 2018, Lundberg et al.,forthcoming). Hence, NRS could have a particular role as target species for public engagement and environmental education programs. In such cases, it is not essential whether protection of the species makes economic sense in that location, but what counts is a sense of responsibility for securing something unique and characteristic to the nature of the local region. Therefore, we emphasize that the choice of the NRS method, as well as the prioritization approach behind it, should depend on the purpose for which NRS are identified.

Deriving national responsibility species from spatial prioritization analyses provides an additional tool available to conservation practitioners and researchers. Linking the practical and intuitive idea of responsibility species with spatial prioritization combines the best of both worlds: It is based on state-of-the-art methodology, yet at the same time, being a simple list of species, it is easy to interpret and implement in practical conservation.

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