RESEARCH ARTICLE

Preserving species populations in the boreal zone in a changing climate: contrasting trends of bird species groups in a protected area network

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Abstract

A protected area network should ensure the maintenance of biodiversity. Because of climate change, species ranges are expected to move polewards, causing further demand for the protected area network to be efficient in preserving biota. We compared population changes of different bird species groups according to their habitat preferences in boreal protected areas in Finland on the basis of large-scale censuses carried out in 1981–1999 and in 2000–2009. Population densities of common forest habitat generalists remained the same between the two periods, while densities of species of conservation concern showed contrasting trends: species preferring old-growth forests increased, but those living on mires and wetlands, and species of Arctic mountains decreased. These trends are most probably connected with climate change, but successional changes in protected areas and regional habitat alteration should also be taken into account. Of species preferring old-growth forests, a larger proportion are southern than among species of mires and wetlands, or of Arctic mountains, most or all of which, respectively, had a northerly distribution. In general, northern species have decreased and southern increased with the exception of northern species of old-growth forests which had not declined. On the other hand, bird species of mires and wetlands decreased also in the northernmost protected areas although mires had not been drained in the region in contrast with southern and central Finland thus indicating that regional-scale direct habitat loss did not cause the decline of these species in the north. It is suggested that climate change effects on species in natural boreal and Arctic habitats most probably are habitat-specific with large differences in response times and susceptibility.

Introduction

A protected area network should ensure the maintenance of species and communities. However, a reserve network is rarely adequate for this purpose (Gaston et al. 2008, Rodrigues et al. 2004). Furthermore, the climate is changing rapidly and, consequently, species ranges are expected to move polewards (Parmesan 2006, Hitch and Leberg 2007, Huntley et al. 2007, Huntley et al. 2008, Zuckerberg et al. 2009) creating further demand for the protected area network to be efficient in preserving biota (Araújo et al. 2004, Hannah and Salm 2005, Hannah et al. 2007). Because of climate change, species distributions shift and networks of reserves may cease to afford protection to those species for which they were originally established (Coetzee et al. 2009, Hole et al. 2009, Araújo et al. 2011). Species and communities in northern boreal and Arctic regions face particular risk from climate change because the Arctic Ocean represents an effective natural barrier to northward range shifts of northern boreal terrestrial species (Virkkala et al. 2008, 2010). Loarie et al. (2009) compared the world's 14 main biomes and protected areas situated within them and showed that climate residence time by 2100 was among the lowest in protected areas situated in boreal forests. This would mean that the climate in protected areas of boreal forests could see the greatest amount of change on a global scale.

Climate-change-driven range shifts are probably among the most dramatic at northern latitudes because of the greater temperature increase projected for these regions (Jetz et al. 2007). For example, in Finland, according to the worst-case climate change scenario, mean annual temperature will increase by as much as 7 °C by 2080 in comparison with the baseline period, 1961–1990 (Jylhä et al. 2004). Annual mean temperatures in Finland increased by 0.7 °C in 1901–2000 with most of the increase at the end of the century (see Jylhä et al. 2004).

An important issue for future conservation planning is what the functionality of the present protected area network is in the face of climate change (Hole et al. 2011). The protected area network should enhance species to survive in a changing climate. Many species are already threatened by intensive human land use that is causing habitat loss.

In northern Europe, the boreal landscape has been intensively utilized; in particular, forestry, alongside agriculture, is the major use of land in vast areas. Natural, old-growth forests have been logged and mires drained for forestry and agricultural purposes. In Finland (Fig. 1) both mires and old-growth forests, in particular, have been regarded as focal habitats for species and communities in terms of conservation, and specific protection programs for both of these habitats have been launched and implemented (OECD 1997, Auvinen et al. 2010). About 12% of all mires and 25% of undrained ones are protected, with a total land area of about 11,000 km^2 (Virkkala et al. 2000). Over 5% (10,700 km^2) of forest land and about half of remaining
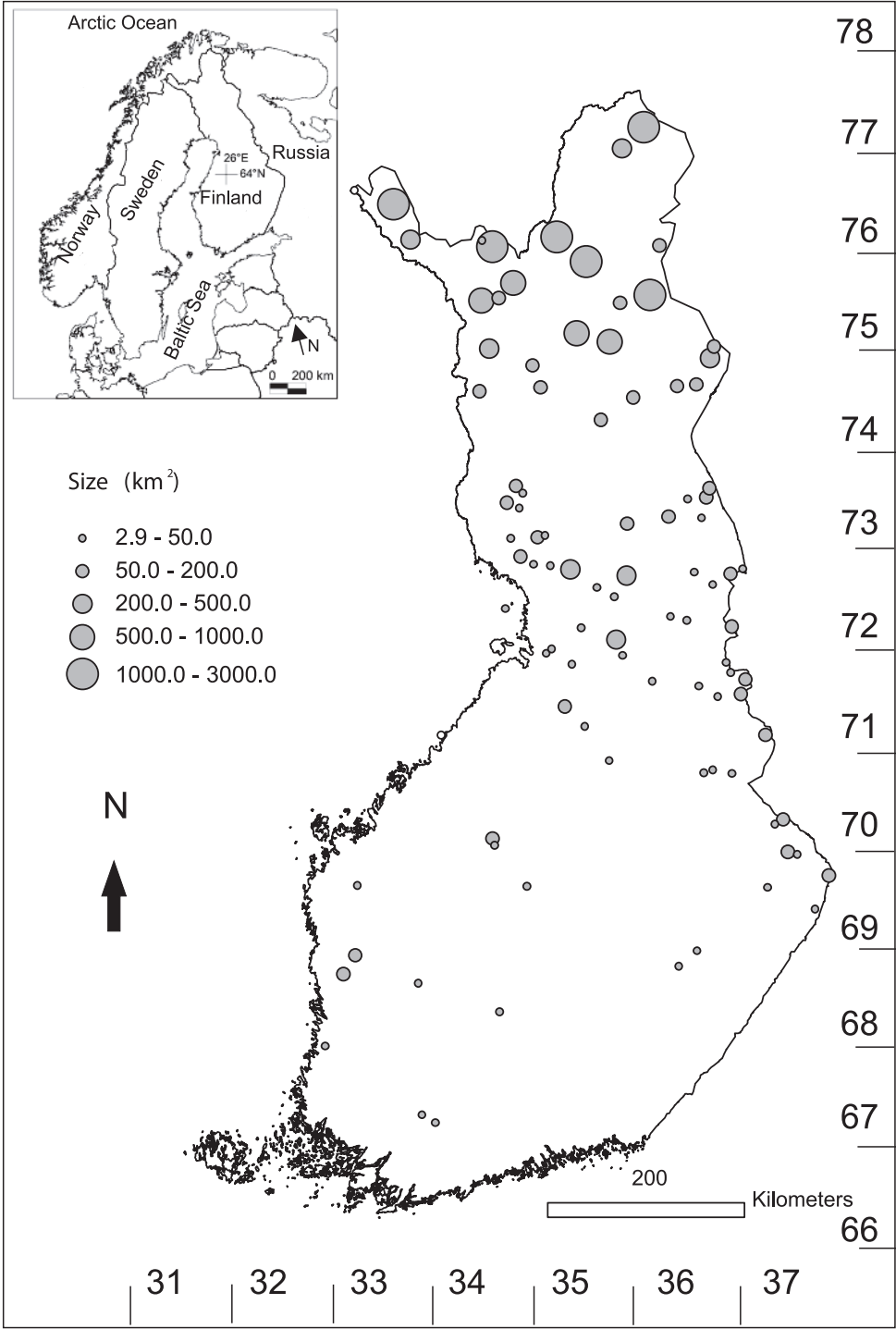
Figure 1. Location of the protected areas in Finland, where bird censuses were carried out both in 1981–1999 and in 2000–2009. Uniform grids (Uniform Coordinate System) used in Finland are presented.

old-growth forests are protected. In spite of the protection programs and many other protected areas (e.g., national parks, wilderness areas, and strict nature reserves) the proportion of protected areas is fairly low in the southern part of Finland, where land use intensity is the highest. In contrast, the protected area network is much larger and more representative in the northern part of Finland (Virkkala et al. 2000, Virkkala and Rajasärkkä 2007). About 80% of the protected land is in northern Finland, in the northern boreal zone (Virkkala et al. 2000).

Direct habitat loss outside protected areas may influence populations of species of conservation concern in protected areas, such as birds breeding on mires and wetlands in southern and central Finland, where over 70% of mires have been drained (Virkkala et al. 2000). In contrast, in the northernmost Finland mires have not been drained (Virkkala et al. 2000), and therefore population changes in protected areas there may not be caused by regional-scale habitat loss. Protected areas are also clearly the largest in the northernmost Finland further reducing the impact of regional human-caused habitat alteration on species populations (see Virkkala 1991). However, we have clear gaps in our knowledge dealing with the effect of the intensity of regional habitat alteration on biodiversity in boreal protected areas.

In this work, we compare in Finnish protected areas population changes of different bird species groups, which are classified according to species habitat preferences. We compare densities by referring to large-scale bird censuses performed in 1981–1999 and in 2000–2009. We have previously shown that northern bird species had declined and southern species increased between the two time slices (Virkkala and Rajasärkkä 2011a, 2011b). In this paper we extend our study of bird population changes in protected areas in relation to species habitat preferences with special emphasis on species of conservation concern. Direct human-caused habitat changes in protected areas have been minor between these time slices because human land use, such as logging and drainage of mires, is not allowed in these areas. In addition to habitat preference, we take into account distribution patterns of species. Here we address the following questions: How successful and efficient has the foundation of boreal protected areas been in terms of maintenance of species populations? Does the protected area network manage to preserve the species of conservation interest – i.e., particularly species preferring old-growth forests and species of mires and wetlands – in a changing climate?

Because land use intensity outside protected areas is different in the different parts of the country, we compare population changes of bird species groups also by taking the location of protected areas into account in order to separate the possible effects of regional habitat alteration (direct habitat loss and degradation outside protected areas) and climate change effects. If regional habitat alteration was the primary cause for population changes, the negative population changes should be more pronounced in the southern than in the northern protected areas both due to more intensive land use outside protected areas and smaller size of reserves in southern Finland. On the other hand, as a consequence of warming climate southern species are predicted to increase and northern species to decline (Jiguet et al. 2010, Kujala et al. 2011).

Material and methods

Protected areas

The total area of reserves (N = 96) in Finland (60–70°N, 21–31°E, Fig. 1) in which bird counts were done was 22,493 km^2, with the protected areas studied ranging in size from three to 2,524 km^2 (mean = 234.3 km^2, median = 51.6 km^2). Logging or drainage of mires is prohibited in the protected areas, so forestry is not allowed in these areas. Reindeer herding is a common use in northern Finnish protected areas. The protected areas studied accounted for over 60% of the land area of Finnish protected areas. Six areas were smaller than 10 km^2 and six larger than 1,000 km^2. The latter largest areas included four wilderness areas and two national parks in northernmost Finland. Twenty-four protected areas were studied in the southern half of Finland (total size: 910 km^2) and 72 in the northern half (total size: 21,583 km^2, see Fig. 1). Most of the protected land is in northern Finland (Virkkala et al. 2000, Virkkala and Rajasärkkä 2007). Forests cover 56% of the land in the reserves studied, with the rest being open mires and mountain areas. In southern half of Finland forests covered 70.0% and in northern half 55.4% of the land in the protected areas. Over two thirds of the protected forest stands are over 100 years old (Virkkala et al. 2000).

Bird censuses

Land birds in protected areas were counted by means of the Finnish line transect census method (Järvinen and Väisänen 1976), which is suitable for counting birds over large areas (Väisänen et al. 1998, Virkkala and Rajasärkkä 2007). The line transect method applies a one-visit census in which birds are counted during breeding season along a transect with an average length of 5–6 km.

The census is carried out in June in the early morning, when the singing activity of birds is highest. In the line transect method, a 50-meter-wide main belt along the walking line (25 m on each side) and a supplementary belt outside the main belt are separated. The latter covers all birds observed outside the main belt (e.g., Järvinen and Väisänen 1976, Järvinen et al. 1991, Väisänen et al. 1998, Virkkala 2004). In the Finnish line transect, densities of species based on the observations in the censuses are calculated in standard units of pairs/km^2. A pair was inferred from a male heard singing, from an otherwise observed male or female or from a group of fledglings according to the instructions of the Finnish line transect census (for details, see Järvinen and Väisänen 1976, Järvinen et al. 1991).

Densities of bird species (pairs/km^2) were calculated on the basis of observations in the whole survey belt, including both main and supplementary belts. Species-specific correction coefficients were used in the density calculation. These coefficients vary according to the proportion of main belt observations to all survey belt observations.

The density of a species (D, pairs/km^2) based on the Finnish line transect census was calculated as:

D = K × N/L, (1)

where K = species-specific correction coefficient, N = number of observations of a species on the whole survey belt, and L = transect length (in km). The species-specific correction coefficient (K) was calculated as (Järvinen and Väisänen 1983):

K = 40 – 40 √ (1– p), (2)

where p = proportion of main belt observations (range 0–1); for details of the calculations, see Järvinen and Väisänen (1983).

The species-specific correction coefficient takes into account the differing audibility and other detectability of different species (Järvinen and Väisänen 1983). The value of this coefficient is low for a species for which only a small proportion of all observations come from the main belt (e.g., the cuckoo *Cuculus canorus*). By contrast, the coefficient's value is high for species for which a large proportion of the observations are made in the main belt (e.g., the capercaillie *Tetrao urogallus*). In addition, detectability of a species may change during the breeding season, such as in the case of the black grouse *Tetrao tetrix*, of which the lekking period with singing (lekking) males usually ends by mid-June (see Appendix). All correction coefficients used in this study were calculated on the basis of line transect data collected from protected areas in Finland and neighboring countries in the boreal and hemiboreal vegetation zones. Species-specific correction coefficients used are presented in the Appendix.

The total length of line transect censuses in the protected areas was 6,587 km in 1981–1999 and 5,087 km in 2000–2009. Birds were counted in 96 areas, in which in both periods the total length of transects was at least 10 km (see Fig. 1). The median total length of transect kms in a protected area was 45.0 km in 1981–99 and 33.6 km in 2000–2009. The mean number of years that censuses were carried out in each protected area was 3.7 (median = 3) in 1981–99 and 2.4 (median = 2) in 2000–2009. The median census year was 1992 in the first and 2006 in the second period, making the average time span in the study 14 years. The same transects were not repeated, but censuses in each protected area included the same proportion of habitats in the two periods. Transects covered all main habitats in each studied protected area relative to each habitat's proportion.

Analyses

Bird species were divided into classes according to habitat preferences, in line with the classification applied by Virkkala et al. (1994) and Väisänen et al. (1998). In these classifications different groups of species of mires and wetlands were combined in the present study, as too were different groups of species of deciduous forests and species of bushes. Species of Arctic Lapland grouped together by Väisänen et al. (1998) were divided into species of Arctic mountain heaths and species of mires and wetlands.

The study used, all told, seven groups of species categorized by habitat preferences (see Appendix): (1) forest habitat generalists, (2) species of coniferous forests, (3) species preferring old-growth or mature forests, (4) species preferring deciduous forests

and bushes, (5) species of mires and wetlands, (6) species of cultivated areas, and (7) species of Arctic mountain heaths. Many species of cultivated areas also breed in natural habitats such as the fieldfare *Turdus pilaris* and hooded crow *Corvus corone cornix* in forests or the curlew *Numenius arquata* on mires. In total 148 species were included in the analyses. All land birds observed along the transects were included in these habitat preference groups except the swallow *Hirundo rustica* and the house martin *Delichon urbica*, which breed on buildings and were excluded.

Bird species were categorized also according to their distribution (see Appendix). Distribution pattern (southern or northern) was classified in terms of distribution and regional density variation in Finland (Väisänen et al. 1998). Species without any northward or southward pattern in their regional density or species with wide-ranging sporadic distribution were regarded as a separate class ('whole country').

Densities of species between the two time periods were compared pairwise in each protected area via either paired *t*-test or non-parametric Wilcoxon signed rank test. A non-parametric test was adopted when the prerequisites for use of a parametric test were not fulfilled. For these analyses species densities were summed in each of the habitat preference class before pairwise comparison. Because the statistical tests were not independent between the comparisons, significant differences were based on sequential Bonferroni correction (Rice 1989).

Next, in a combined analysis, habitat preference class and distribution pattern were compared through repeated measures analysis of variance (ANOVA). Time (periods) represents here a quantitative, repeated factor, the effects of which can be examined via within-subject contrasts (e.g., Gurevitch and Chester 1986; Quinn and Keough 2002). Habitat preference class and distribution pattern were regarded as between-subjects factors in the analysis. We took into account in the analysis all species observed in at least two thirds of the protected areas in both periods (in 64 out of 96 areas, 37 species). This was essential because parametric statistical analyses were adopted and the other, less common species were non-normally distributed in protected areas as a result of the high proportion of zero classes. Bird pairs in these 37 common species studied constituted the vast majority of the bird communities, 88% of all bird pairs in protected areas.

Change in the average density of each habitat preference group was compared in each of the protected area between the two time slices (n = 96). Percentage changes in density in each of the protected areas were used. Percentage changes above and below 100% are not strictly comparable; for example, a doubling increase from 100 gives a value of 200, but a similar decrease to half that yields 50. To avoid this discrepancy, we used logarithmic ratio (log ratio) of per cent change in densities, where, for example, 100% increase in density from 1981–1999 to 2000–2009 would be log (200/100) = +0.301 and 50% decrease is log (50/100) = –0.301. In a linear regression analysis we used location (south-north) and size of a protected area (log-transformed) as predictive (explanatory) variables for the temporal density changes of the different bird groups. South-north location and size of protected area are positively correlated (r = 0.629, p<0.001) i.e. largest protected areas are situated in the northernmost Finland.

Densities of bird species between the two time periods were compared also based on IUCN threat categories in Finland (Rassi et al. 2010), which included threatened and near threatened species and species of least concern (see Appendix). Critical, endangered and vulnerable classes were regarded as threatened.

Results

The mean temperature of the coldest month (February) and that of April–June essential for bird species (see Heikkinen et al. 2006, Virkkala et al. 2008) were compared from Finnish Meteorological Institute data. The mean temperature of the coldest month rose by 0.8 °C (1981–1999: –9.46 °C, 2000–2009: –8.66 °C) and that for April–June by 0.7 °C in Finland (1981–1999: 6.71 °C, 2000–2009: 7.43).

Population changes of species groups based on habitat preferences in 1981–1999 and in 2000–2009 are presented in Table 1. The mean density of forest habitat generalists did not change from 1981–1999 to 2000–2009. Forest habitat generalists accounted for more than half of all breeding bird pairs (55–56%) in protected areas. Densities of species of coniferous forests and species preferring old-growth and mature forests increased, while species of deciduous forests and bushes, species of mires and wetlands, and species of Arctic mountains decreased between the two time slices (see Table 1). In proportional terms, the largest decrease was in species of Arctic mountains, which declined to less than half (–57%), and the largest increase in species preferring old-growth and mature forests, which increased by 29%.

Densities of southern species increased significantly in forests habitat generalists, in species of coniferous forests and in species preferring old-growth or mature forests from 1981–1999 to 2000–2009 (Table 2). Densities of northern species decreased significantly in forest habitat generalists, in species of coniferous forests and in species of mires and wetlands. Species of coniferous forests distributed across the whole country increased (Table 2).

Table 1. Mean densities (pairs/km² ± standard error) of bird species groups with different habitat preferences in 1981–1999 and in 2000–2009. Statistical test (N = 96) by paired t-test or Wilcoxon signed rank test (species of Arctic mountains). Number of species in each species group in parentheses.

Species group	1981–1999	2000–2009	t	z	p[a]	Ranks[b]
Forest habitat generalists (15)	63.15±3.66	60.38±3.02	1.170	–	0.245	–
Species of coniferous forests (26)	17.75±1.42	20.65±1.49	4.079	–	**<0.001**	–
Species preferring old-growth or mature forests (14)	2.83±0.21	3.64±0.27	3.848	–	**<0.001**	–
Species preferring deciduous forests and bushes (23)	3.27±0.67	2.49±0.52	2.633	–	**0.010**	–
Species of mires and wetlands (36)	22.41±2.47	18.65±2.04	3.210	–	**0.002**	–
Species of cultivated areas (23)	2.27±0.24	2.88±0.34	2.083	–	0.040	–
Species of Arctic mountains (11)	0.37±0.15	0.16±0.07	–	2.561	**0.010**	7/23/66

[a] Significant differences (bold) are based on sequential Bonferroni correction.
[b] Ranks between 2000–2009 and 1981–1999: positive/negative/tied.

Table 2. Densities of species groups with different habitat preferences (p/km² ± s. e.) according to distribution pattern. Statistical significance is based on paired t-test (df = 95) or Wilcoxon signed rank test (N=96). Number of species in each group in parentheses. All Arctic mountain species are northern (see Table 1) and no species of cultivated areas is northern.

Distribution pattern	1981–1999	2000–2009	t	z	p[a]	Ranks[b]
Forest habitat generalists						
Southern species (5)	13.76±1.96	18.19±2.11	4.686	–	**<0.001**	–
Northern species (2)	12.93±0.93	10.06±0.82	3.924	–	**<0.001**	–
Whole country[c] (8)	36.46±2.12	32.13±1.59	2.611	–	0.010	–
Species of coniferous forests						
Southern species (16)	11.61±1.23	14.34±1.36	4.915	–	**<0.001**	–
Northern species (6)	2.41±0.22	1.63±0.18	4.569	–	**<0.001**	–
Whole country (4)	3.74±0.24	4.68±0.29	4.068	–	**<0.001**	–
Species preferring old-growth or mature forests						
Southern species (6)	1.08±0.14	1.68±0.19	5.385	–	**<0.001**	–
Northern species (6)	0.99±0.12	1.08±0.12	0.770	–	0.443	–
Whole country (2)	0.76±0.07	0.88±0.08	1.182	–	0.240	–
Species preferring deciduous forests and bushes						
Southern species (20)	2.70±0.66	2.06±0.52	2.386	–	0.019	–
Northern species (2)	0.56±0.20	0.42±0.13	–	1.304	0.192	21/15/60
Whole country (1)	0.01±0.00	0.01±0.01	–	0.350	0.727	6/7/83
Species of mires and wetlands						
Southern species (8)	0.02±0.01	0.02±0.01	–	0.751	0.452	14/16/66
Northern species (22)	19.08±2.26	15.63±1.86	3.248	–	**0.002**	–
Whole country (6)	3.30±0.62	2.99±0.60	1.184	–	0.239	–
Species of cultivated areas						
Southern species (15)	0.52±0.09	0.65±0.12	1.658	–	0.101	–
Whole country (8)	1.75±0.19	2.23±0.26	1.971	–	0.052	–

[a] Significant differences in bold (sequential Bonferroni correction for all the comparisons).
[b] Ranks between 2000–2009 and 1981–1999: positive/negative/tied.
[c] Whole country = species distributed throughout the country.

In the repeated measures ANOVA carried out for the most common 37 species, there was a significant difference both in the habitat preference and in the distribution pattern (Table 3). However, the statistical significance for the distribution pattern (F = 38.16, $p < 0.001$) was much more pronounced than for the habitat preference (F = 3.06, $p = 0.016$; Table 3). Northern species decreased and southern species increased in the different habitat preference classes (Fig. 2). Interaction between factor levels and the two between-subject factors (habitat preference and distribution pattern) was significant ($F = 9.631$, $p < 0.001$), which was mainly due to the fact that species distributed across whole country included both increased and decreased species (see Fig. 2).

The regression model with south-north location and size of protected area as predictive variables explained significantly only population changes of species of coniferous forests, and this species group increased most in the northern Finnish protected areas (Table 4, Fig. 3A). In other species groups location and size of protected area did not affect population changes observed (for species of mires and wetlands, see Fig. 3B).

Table 3. Results of within-subject contrasts of repeated measures analysis of variance (ANOVA). Factor levels (within-subject): density in 1981–1999 and 2000–2009; between-subjects factors: habitat preference (habitat), distribution pattern. * = Interaction between factor levels and different between-subjects factors.

Source	[a]df	[b]MS	F	p
Factor	1	27.331	6.030	0.014
Factor*species	1	5.548	1.224	0.269
Factor*protected areas	1	20.926	4.617	0.032
Factor*habitat	2	13.878	3.062	0.016
Factor*distribution	2	172.970	38.161	<0.001
Factor*habitat *distribution	3	43.654	9.631	<0.001
Error (factor)	3539	4.533		

[a]df = degrees of freedom.
[b]MS = mean squre.

Table 4. Regression analyses based on location (south-north coordinates) and size of a protected area (log-transformed) as predictors affecting the temporal density changes of species groups with different habitat preferences. $df_{regression}$ = 2, $df_{residual}$ = 93. The values (B) and significance (based on t-test) of the standardized coefficients are presented. Standardization of the coefficient shows which of the independent variables have a greater effect on the dependent variable, when the variables are originally measured in different units (see Quinn and Keough 1982).

Species group	[a]r²	[b]MS	F	p	Standardized coefficients					
					Location			Size		
					B	t	p	B	t	p
Forest habitat generalists	0.044	0.069	2.145	0.123	0.254	1.944	0.055	–0.087	0.668	0.506
Species of coniferous forests	0.154	0.499	8.480	<0.001	0.365	2.976	0.004	0.042	0.340	0.735
Species preferring old-growth or mature forests	0.017	0.145	0.800	0.452	–0.137	1.039	0.302	0.012	0.093	0.926
Species preferring deciduous forests and bushes	0.004	0.092	0.165	0.848	0.060	0.451	0.653	-0.075	0.560	0.577
Species of mires and wetlands	0.015	0.064	0.685	0.507	–0.117	0.882	0.380	–0.006	0.043	0.966
Species of cultivated areas	0.013	0.113	0.628	0.536	–0.110	0.831	0.408	–0.008	0.062	0.951

[a]r² = coefficient of determination
[b]MS = mean square

Densities of both threatened and near threatened bird species decreased significantly from 1981–1999 to 2000–2009, while density of the other species (least concern) did not change between the two time periods (Table 5).
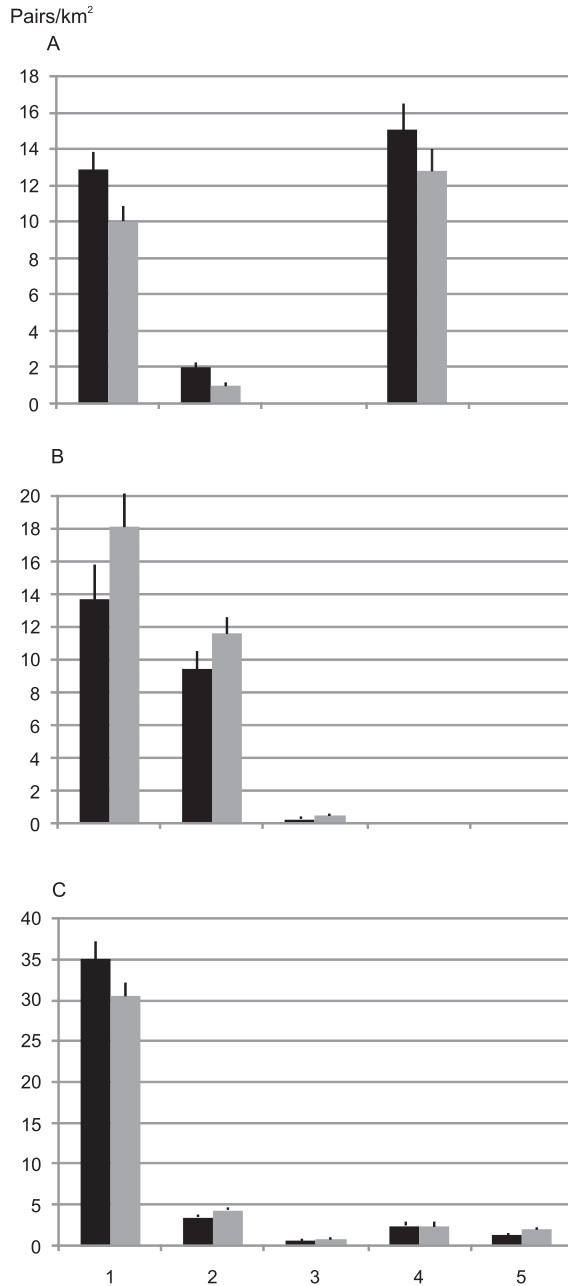
Pairs/km²

Figure 2. Mean density (pairs/km²±S.E.) of different bird species groups (most common species) in protected areas in 1981–1999 (black columns) and in 2000–2009 (gray columns). **1** = forest habitat generalists, **2** = species of coniferous forests, **3** = species preferring old-growth or mature forests, **4** = species of mires and wetlands, **5** = species of cultivated areas. **A** northern species **B** southern species **C** species distributed over the whole country. Northern species preferring old-growth forests, southern species of mires and wetlands, and both southern and northern species of cultivated areas were not included in the analysis due to their rarity or absence.
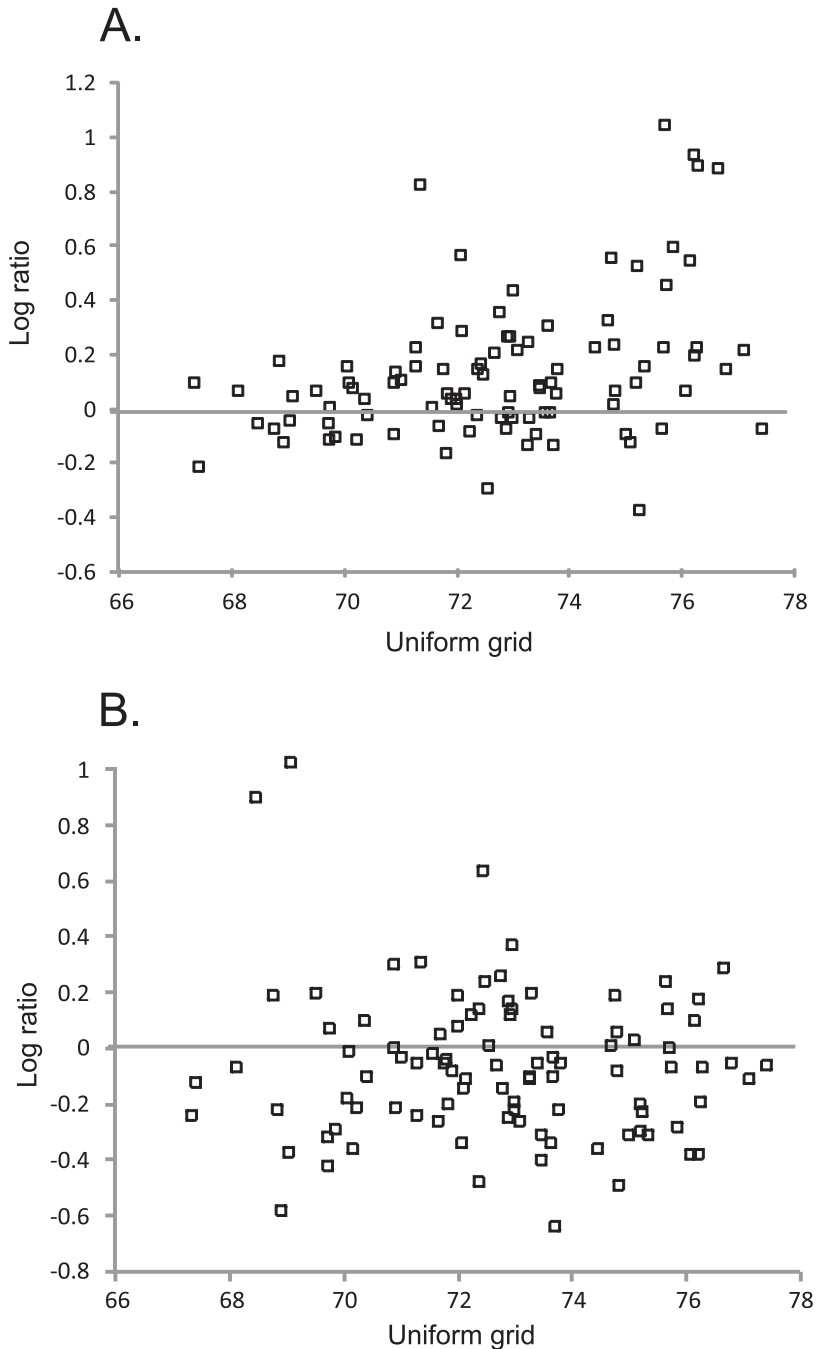
Figure 3. Change in the average density of species of coniferous forests (A.) and species of mires and wetlands (B.) from 1981–1999 to 2000–2009, based on log ratio [log ratio = log (density in 2000–2009/ density in 1981–1999)] in each protected area (n = 96) according to location from south to north (for uniform grid, see Figure 1). Values of log ratio above zero (line) show population increase and those below zero population decline in each protected area.

Table 5. Densities (pairs/km^2 ± s.e.) of bird species groups according to IUCN threat status (threatened, near-threatened, least concern, see Appendix) in Finland in 1981–1999 and in 2000–2009. Statistical test (df = 95) by paired t-test. Number of species in each species group in parentheses.

IUCN category	1981–1999	2000–2009	t	p
Threatened (23)	8.53±0.67	5.63±0.50	6.142	<0.001
Near threatened (19)	10.18±0.81	8.25±0.66	3.714	<0.001
Least concern (106)	93.35±5.16	94.97±4.64	0.510	0.611

Discussion

We observed that patterns in the population changes of the different bird species groups varied considerably. Moreover, there were large within-species-group differences in population trends when distribution pattern of species was taken into account. At a European scale Gregory et al. (2009) observed, based on bird censuses in 1980–2005, that species predicted to expand their ranges due to climate change have increased and species predicted to lose ranges have decreased. Our results of bird population changes in boreal protected areas are in line with the results of Gregory et al. (2009), but it is further suggested that climate change effects on species in natural boreal and Arctic habitats most probably are habitat-specific with large differences in response times and susceptibility.

The species of greatest conservation interest in terms of land-use pressures showed interesting patterns: species preferring old-growth or mature forests have contrasting trends with the species of mires and wetlands in the protected area network. Preserving old-growth forests seem to have clearly benefited species preferring these habitats in Finland, while species of mires and wetlands have decreased in spite of fairly large-scale protection of these habitats. However, an important point here is that a much larger proportion of bird pairs in species preferring old-growth forests are southern (38–46%) than the equivalent figure among species of mires and wetlands (0.1%). There was a general pattern in the different species groups that northern species had decreased and southern species had increased, which is in line with the predictions of range shifts of species both in Europe and in Fennoscandia (Huntley et al. 2007, Huntley et al. 2008, Virkkala et al. 2008, 2010, Kujala et al. 2011, Barbet-Massin et al. 2012).

Also species of Arctic mountains have decreased, although about 90% of mountain heaths are within protected areas (Virkkala et al. 2000). All species of Arctic mountains and 85% of bird pairs of mire and wetland species were northerly distributed. This further suggests that climate change has a considerable effect on population changes of these species groups. Species of Arctic mountains is also the species group with clearly the highest proportion of threatened species: over half (six species) of the 11 species is regarded as critical, endangered or vulnerable with additional three species being near threatened (see Appendix).

Moreover, species of mires and wetlands have decreased also in large protected areas situated in northernmost Finland (see Fig. 3B), in which region (north of the uniform grid 74 in Fig. 1) mires have not been ditched at all (Virkkala et al. 2000). Therefore, the decrease of species of mires and wetlands in the northern protected

areas cannot be explained to be caused by drainage of mires outside protected areas. Northern Finnish habitats both in protected and in unprotected areas are grazed by reindeers, which may have an effect also on bird species densities.

In a recent study, Kujala et al. (2011) further showed in the most common bird species that northerly-distributed species were well-represented in the Finnish protected area network, but the population trends of these species are currently declining in Finland most probably reflecting changes in climate. In addition, southerly-distributed species with poor coverage in protected areas are increasing.

Forest habitat generalists had not increased, in contrast with the other species group in which species have large habitat amplitudes – namely, species of coniferous forests. These species occur in variable coniferous woods without strict habitat preferences. As in the comparison of species groups of greatest conservation interest (species preferring old-growth forests vs. species of mires and wetlands), a much larger proportion of species and bird pairs of coniferous forests are southern (about 55%) than among forest habitat generalists (20–30%, see Table 2), which probably explains the different patterns of population changes in these species groups. The increase of species of coniferous forests was most pronounced in the northernmost protected areas (Fig. 3A). This probably reflects the fact that southern bird species have increased most at their northern range boundary occurring in northernmost Finland (Virkkala and Rajasärkkä 2011b). Populations of species preferring coniferous forests are probably also affected by the overall increase in coniferous wood volume due to, for example, drainage of mires and increased annual increment of the growing stock (wood volume), which is also affected by increased temperatures. Moreover, in a previous study, Virkkala and Rajasärkkä (2011a) showed that migratory patterns could not explain the population changes observed among bird species in Finnish protected areas.

The decrease of species of deciduous forests and bushes may be caused by the fact that many of these species occur in early succession forest habitats which have changed as a consequence of forest succession in many of the studied protected areas during the study period. Many bird species prefer early succession forest habitats and disappear or decline, when forest maturates (see Helle 1985, Helle and Mönkkönen 1985).

Forest succession probably also affects the increase of southern old-growth forest species, because in southern Finland many forests in protected areas have previously been managed and therefore forests are much younger there than in northern Finnish protected areas (Virkkala et al. 2000), where old-growth forests were prevailing already at the time of foundation of protected areas. In southern Finland, previously managed and younger forests in reserves have matured and developed probably as more suitable to the species preferring old-growth or mature forests during the average study period of 14 years. However, according to the comparison of the results of Finnish bird atlases in 1974–89 and in 2006–2010, many of the southern species of old-growth and mature forests have increased and enlarged their ranges in Finland, such as the red-breasted flycatcher *Ficedula parva* and treecreeper *Certhia familiaris* (see Valkama et al. 2011).

Bird species populations in protected areas have thus been affected by climate change, successional habitat changes in protected areas and probably also landscape-level habitat

changes outside protected areas. The latter two factors cannot however explain the general, overall increase of southern species and decrease of northern species (Tables 2 and 3 and Fig. 2). Moreover, two-thirds of the threatened species in our data (15/23) are northern.

There might be a relation between climate niche, habitat niche and range size affecting population trends of species. Barnaugaud et al. (2012) observed in studying climate and habitat niches of French birds that species with narrow thermal breadths were also more often habitat specialists. We did not study climate niches of bird species but in general southern species probably have larger ranges and also larger climate niches than northern species. So there may be a positive correlation between climate niche and population trend, but this issue should be properly studied.

Specialist species might be more susceptible to climate change than habitat generalists (Jiguet et al. 2007, Devictor et al. 2012). However, in our study specialist species of old-growth forests had not declined in contrast with specialists of wetlands and mires. In addition, forest habitat generalists consisted of both declined northern species and increased southern species. So there seems not to be any general pattern between habitat niche breadth and population trend of species in our data, but also this issue should be studied in more detail.

Densities of northern species have generally declined (Virkkala and Rajasärkkä 2011a). However, population densities of northern species preferring old-growth forests remained the same, so the patterns are not always unambiguous: different species and species groups are affected in a different manner by several factors, including climate change and land use. For northern species preferring old-growth forests, the large northern protected area network – over 40% of forests are protected in northernmost Finland (Virkkala et al. 2000, Virkkala and Rajasärkkä 2007) – may have mitigated the negative effects of climate warming. This might be because climate factors may affect old-growth forests more slowly than they do mires or Arctic mountain heaths. Thus, also the response time to changes in climate and land cover varies between species and between species groups. For some species conditions become more suitable through both climate-induced and land-use changes while other species are highly susceptible to changes in their habitat (see also Matthews et al. 2011).

In a recent work dealing with protected area networks in Canada, it was observed that butterfly populations had declined both in protected and in non-protected areas, suggesting that existing reserve networks have provided little buffer against the impacts of climate change on butterfly species richness (Kharouba and Kerr 2010). In Finnish protected areas, the same seems largely to hold true for northerly distributed birds, since these birds have mostly, with the exception of species preferring old-growth forests, declined regardless of their habitat preferences. On the other hand, southern species preferring old-growth forests have increased in Finnish protected areas. So the pattern maybe more complicated than that observed by Kharouba and Kerr (2010) in Canada. It seems that both distribution pattern and habitat preferences of species affect population changes of species in boreal protected areas, in addition to the quantity and quality of protected areas.

Mires and mountain heaths change more rapidly in consequence of climate warming than old-growth forests, for which reason populations on mires and mountain heaths are also more affected by climate change. For example, in northernmost Europe, wet, structurally diverse palsa mires created by permafrost are expected to decline and become more homogeneous fairly rapidly in the coming decades as a consequence of climate warming (Fronzek et al. 2010), resulting in decreased abundance of bird populations, such as many wader species found in these ecosystems (Luoto et al. 2004). Furthermore, species-rich boreal aapa fens are changing into drier bogs because of climate warming (Tahvanainen 2011). As a result of upward-advancing treelines in Scandian mountains, treeless heaths are predicted to decline by 75–85%, with most of the remaining areas being slopes and boulder fields (Moen et al. 2004). As a consequence of climate change, vegetation changes in Arctic mountains are predicted to be considerable and rather rapid (Sormunen et al. 2011). On the other hand, stand age of natural old-growth forests in Fennoscandia is typically over 200 years or even 300 years with stand cohorts of over 150 years dominating (Kuuluvainen 2002, Pennanen 2002). Therefore, climate probably also affects bird communities in mires and on mountain heaths more rapidly than those in old-growth coniferous forests.

In conclusion, the protected area network is highly dependent on the susceptibility of focal habitats to climate change effects. If the focal habitats are expected to change rapidly because of climate change (as with mires and heaths), the protected area network appears more vulnerable in preserving species in the focal habitats than if the time lag in the effects of climate change on habitat is presumed to be long (as with old-growth forests).

Acknowledgements

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Appendix

Bird species' census data in Finnish protected areas (doi: 10.3897/natureconservation.3.3635.app). File format: MS Word Document (doc).

Explanation note: Mean densities and number of observations of species in 1981–1999 and in 2000–2009.

RESEARCH ARTICLE

National responsibilities for conserving habitats – a freely scalable method

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Abstract

Conservation of habitats is a major approach in the implementation of biodiversity conservation strategies. Because of limited resources and competing interests not all habitats can be conserved to the same extent and a prioritization is needed. One criterion for prioritization is the responsibility countries have for the protection of a particular habitat type. National responsibility reflects the effects the loss of a particular habitat type within the focal region (usually a country) has on the global persistence of that habitat type. Whereas the concept has been used already successfully for species, it has not yet been developed for habitats. Here we present such a method that is derived from similar approaches for species. We further investigated the usability of different biogeographic and environmental maps in our determination of national responsibilities for habitats. For Europe, several different maps exist, including (1) the Indicative European Map of Biogeographic Regions, (2) Udvardy's biogeographic provinces, (3) WWF ecoregions, and (4) the environmental zones of Metzger et al. (2005). The latter is particularly promising, as the map of environmental zones has recently been extended to cover the whole world (Metzger et al. in press), allowing the application of our methodology at a global scale, making it highly comparable between countries and applicable across variable scales (e.g. regions, countries). Here, we determined the national responsibilities for 71 forest habitats. We further compared the national responsibility class distribution in regard to the use of different reference areas, geographical Europe, Western Palearctic and Palearctic. We found that the distributions of natural responsibility classes resembled each other largely for the different combinations of reference area and biogeographic map. The most common rank in all cases was the "medium" rank. Most notably, with increasing size of the reference area, a shift from alloca-

tions to a basic rank to allocations to a medium rank (from 1:4 to 1:1) was observed. The least frequent rank was the "very high" category. The methodology to determine national responsibilities presented here is readily applicable to estimate conservation responsibilities for habitats of the EU25 countries. It should be based on the environmental zones map and should use Europe as the reference area. It then provides a tool to allocate funds, direct conservation actions in the most sensible way, and highlight conservation-relevant data gaps.

Introduction

Despite numerous legal commitments, resources for habitat conservation remain scarce, requiring a prioritization of conservation efforts. In contrast to species, for which a range of different approaches have been developed (Schnittler et al. 1994, Couturier 1999, Schnittler and Günther 1999, Beissinger et al. 2000, Carter et al. 2000, Coates and Atkins 2001, Keller and Bollmann 2001, 2004, Schnittler 2004, Brooks et al. 2006, Schmeller et al. 2008a, b, c), fewer methods are available for habitats (but see Schnittler et al. 1994, Essl et al. 2002, Traxler et al. 2005). However, European countries are responsible for conservation of natural and semi-natural habitats, as they have adopted the obligations of the Convention on Biological Diversity (CBD). Within the European Union, the principal legal instrument for habitat conservation is the 1992 Habitats Directive (92/43/EEC) which has been transposed into national law by all 27 Member States. The directive is an EU implementation of the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats; see also Evans 2012). At the European Council in Göteborg in 2001, the Heads of State made a commitment to "halt biodiversity loss by 2010" and the EU has adopted a biodiversity strategy with clear targets for habitat conservation (CEC 2006, 2012).

Priority areas of conservation importance were defined using the concept of biological hotspots for large biomes (Mittermeier et al. 1998). At finer geographical scales, red lists are the most commonly used tool for conservation assessment as they explain the complex phenomenon "endangerment" in a simple way (The Nature Conservancy 1988, IUCN 1996, IUCN 2001), granting high public acceptance (Schnittler and Günther 1999). The resulting threat status is also taken as a measurement for conservation priorities. However, red lists may at best be a suboptimal tool for setting conservation priorities in a country or region as the threat status does not always reflect actual conservation needs (Gärdenfors 2000, 2001, Mehlman et al. 2004, Eaton et al. 2005). That is especially true from a subsidiary point-of-view, from which it is clearly more desirable to focus national conservation efforts on the habitat types centred in the respective country. As a response, the concept of national responsibility as a complementary tool was developed for species (Schnittler et al. 1994, Schnittler and Günther 1999, Schnittler 2004, Schmeller et al. 2008c).

The assessment of national responsibilities covers the notion of the importance of a region for the conservation of biodiversity in respect to its irreplaceability (Brooks et al. 2006). Hence, national responsibility serves as a proxy for measuring the probability of global persistence for a given habitat, when a habitat of the focal area (e.g. nation or region) is lost. Hence, if the disappearance of a habitat type in the focal nation affects the global persistence particularly strongly, a nation's responsibility for that habitat is high or even very high. The nation's responsibility for a habitat would be considered low, if overall persistence of a habitat is not affected by the loss in that nation. Therefore, determination of national responsibility permits to emphasise international obligations of conservation that may not be obvious on a local level or by using national red lists only. Although the concept has already been used successfully for species, it has, with two exceptions for Europe, not yet been developed for habitats. National responsibility for habitats has been evaluated within the Red List of biotopes of Austria (Essl et al. 2002, Traxler et al. 2005), using the system developed by Schnittler et al. (1994) and for Annex I habitats of the Habitats Directive. However, no information is available on the methodology and the data used (presumably expert opinion; Henle et al. unpublished). Though habitats for which Europe has a high conservation responsibility should receive high priority, each EU country is equally obliged to conserve habitats listed on the Annex I of the Habitats Directive (Council Directive 92/43/EEC; http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:01992L0043-20070101:EN:NOT).

The goal of this contribution is the presentation of a new method to determine national responsibilities for habitats which has been derived from a similar method for species (Schmeller et al. 2008a). We discuss limitations caused by different classifications of habitat types and develop the method in the context of different maps of biogeographical regions and environmental zones. Combining the national responsibility results with red lists or other lists reflecting the conservation status (e.g. status of habitats from reporting required by Article 17 of the Habitats Directive) will allow to determine conservation priorities and/or conservation actions and help in sharing the limited resources in observing and conserving biodiversity. We illustrate the approach for the 71 forest habitat types listed on Annex I of the Habitats Directive.

National responsibility method for habitats

The method to determine national responsibilities for habitats comprises three decision steps. Firstly, the habitat unit is defined; secondly, the distribution pattern of a habitat is determined, meaning its range within and across biogeographic and environmental regions (Figure 1). We used three categories (local, regional, wide), which will be defined below. The distribution pattern of a habitat is central for the assessment of national responsibilities because it measures the importance of the habitat within a focal area. The variation in distribution patterns in relation to biogeographic zones reflects the adaptability of the habitat to different climatic and environmental
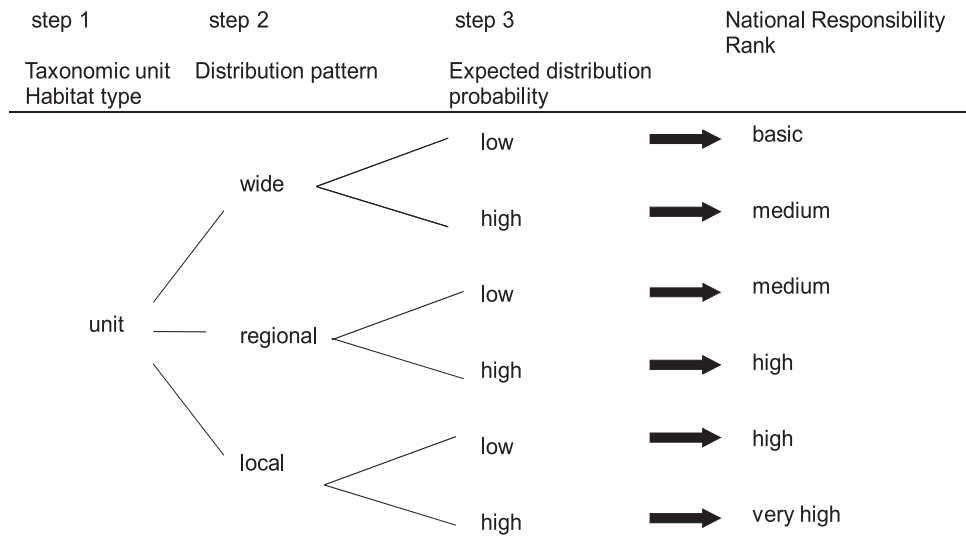
step 1	step 2	step 3	National Responsibility Rank
Taxonomic unit Habitat type	Distribution pattern	Expected distribution probability	

Figure 1. Decision tree for the determination of national responsibilities.

conditions. Therefore, a widely distributed habitat can be assumed to be more robust against environmental change, whereas habitats found only in one or two biogeographical regions may face higher pressure of disappearance due to limited adaptability and due to natural and anthropogenic catastrophic events. Our method also takes into account that different parts within a distribution area may play different roles for the overall conservation of a taxon, habitat, or a species (Hanski et al. 1995, Brooks et al. 2006). For example, areas with high quality examples of a habitat type are usually small and rare, with the result that some parts of a habitat's distribution range are more important for the global persistence of a habitat type and the species dependent on that habitat than others, hence having a high international importance for conservation (Schmeller et al. 2008c). To determine the international importance of a localized habitat type for its global persistence, existing methods used several range-based criteria, such as proportional distribution, relative abundance, or location of the distribution center (Schnittler 2004, Schmeller et al. 2008c). Here, we focus on distribution pattern (step 2) and proportional distribution (step 3). The third step determines the importance of a habitat distribution within a focal area as compared to the total distribution or reference area, determining the expected and observed distribution of a habitat, allowing an adaptation to different geographic scales. The distribution pattern and the expected value of occurrence together reflect the importance of a focal area for the global persistence of a habitat. The combination of these 3 steps results in 4 classes of national responsibility (Figure 1). Habitats falling within the same classes should be treated equally in regard to their conservation, as the currently available data is too coarse to make finer adjustments of the categories with less information loss. The application of each of these three steps, while generally straightforward, needs to take several issues into consideration.

Step 1: Habitat type

Habitats have both an inherent variability and variations in how they are interpreted from country to country, and sometimes between regions in the same country (Evans 2010). This means that an EU member state or any other country may be the only country where a subtype occurs even though the habitat itself is very widespread. This is an important point, when interpreting the results of a national responsibility assessment.

Definitions also differ between international organizations, such as FAO, CBD, and UNFCCC (Schoene et al. 2007), and between non-EU European countries, e.g. for forests (EEA 2006). In these definitions height, tree density, area, and species composition play a major role and definitions are far from being standardized (Hall et al. 1997). In Europe differences also exist between countries in defining grazing land; in some countries heath lands (low scrub) are included, in others they are excluded, depending on farming practice. These definitions are important when assessing forest decline, land conversion, or CO_2 sequestration (Bunce et al. 2010), and national responsibilities. These differences are also visible from the wide range of existing phytosociological vegetation classifications (e.g. Becking 1957, Tichý 2002, Jennings et al. 2009). Phytosociology has had an important influence on the Habitats Directive with some two thirds of the habitats of Annex I having a reference to a syntaxa either in the name or definition. Phytosociology has also been important in the implementation of the directive in most EU countries, as shown by e.g. Biondi et al. (2012). Nonetheless, many nations apply a detailed local habitat classification, such as Germany (the German biotope classification: Riecken 2006) and Hungary (Hungarian National Habitat Classification System Á-NÉR: Fekete et al. 1997, Molnár et al. 2007).

National habitat classifications are usually structured in a hierarchical order consisting of subclasses, which allows a detailed distinction of habitat types dependent on several variables. For example, the German classification, which was used to compile the Red List of German habitats (Riecken 2006), divides deciduous forests in several sub-classes according to local edaphic characteristics, water dependency, site elevation, or species composition. In this way, parameters are interrelated with each other and deciduous forest types are thus presented in a hierarchical order, which allows increasingly detailed distinctions when downscaling from the broadest class to a finer subclass. However, the application of national habitat classifications on surveying habitats leads to distribution information, which is coherent only within national boundaries. Detailed international habitat classifications have been developed for specific habitat groups, such as Baltic Sea habitats or wetlands, (e.g. HELCOM habitat classification 1998, Ramsar Classification System for Wetland Types 2009). However, in order to determine national responsibilities for all habitat groups, a unified classification including all habitat types occurring within the focal geographic area is required.

International classifications, which are not restricted to specific habitat groups and covering a larger geographic range, have been published for Europe and the Palearctic. The CORINE (CORINE: Coordinated Information on the Environment; Moss and Wyatt 1994) program which started in the 1980s has produced classifications of land use and of

biotopes. CORINE Land Cover uses remote sensing to produce land cover maps at regular intervals using a typology with 44 units, whilst the CORINE biotopes classification distinguishes habitats at a finer scale (Devillers et al. 1991, Moss and Wyatt 1994). The maps from CORINE Land Cover are not sufficiently detailed to be of use for assessing national responsibilities. For example only three types of natural forests are distinguished in comparison to 71 in the Habitats Directive. The CORINE biotopes classification is sufficiently detailed but there is no corresponding data on distribution of the habitat types.

The European Nature Information System (EUNIS; eunis.eea.europa.eu/) provides a database on habitats, species and protected areas which is built on a hierarchical habitat classification (Davies et al. 2004). EUNIS aims to provide a comprehensive classification for European habitats, including a framework of descriptions using habitat parameters and presents information on habitats including descriptions, cross-references with other classification systems and gives some distribution data based on protected sites from which the habitat has been reported. At present, habitat distribution data available from EUNIS is not sufficient for use to determine national responsibility for most habitats.

Annex I of the Habitats Directive lists habitats for which Sites of Community Interest (SCI) must designate sites as part of the NATURA 2000 network as SACs (Evans 2012) and Article 17 of the European Habitats Directive requires all Member States to monitor and report on their conservation status. Although Annex I is not a classification (the habitats come from several classifications, see Evans 2006, 2010, Bunce et al. 2012), it does include a wide range of natural and semi-natural habitats. Reports from the 2nd reporting period (2001–2006) are available (ETC/BD EIONET webtool at http://biodiversity.eionet.europa.eu/article17/habitatsreport/, ETC/BD 2008b and EEA 2009), including assessments of the conservation status of habitats. The Article 17 database (http://www.eea.europa.eu/data-and-maps/data/article-17-database-habitats-directive-92-43-eec) provides information on distribution areas of the habitat types reported by Member States. The national reports are in a variety of formats, but a harmonized set of distribution maps, based on a 10 km x 10 km grid prepared by the ETC/BD, is available. At present the Article 17 database represents the most extensive dataset for habitat distribution and conservation status in the European Union. Although there are many problems associated with the interpretation of the habitats listed in Annex I (Evans 2010, Evans 2012), which can result in unevenness between Member States, basic distribution data gathered under the same framework across the EU25 is available. Therefore, at present the list of 231 habitat types of the Habitats Directive presents the only habitat dataset backed with reasonable data on distribution and extent with which to test the methodology of national responsibilities. The next update of the Article 17 database is due in 2015 and will then include data from all 27 EU Member States.

Step 2: Distribution pattern

In the second step, the distribution pattern of the habitat unit is determined. Generally, the distribution pattern may serve as an approximation of the ability of a habitat

to cope with threat factors, similar to a species' distribution pattern in relation to environmental conditions (e.g. Wiens et al. 1997, McIntyre and Wiens 1999). Hence, the distribution pattern provides information about suitable environments for habitats.

For determining the distribution pattern, the choice of the biogeographical map needs to be considered. For the assessment of habitat distribution patterns across biogeographic regions, we have examined the following maps, (1) the Indicative European Map of Biogeographic Regions (hereafter IEMB; EEA 2006, ETC-BD 2006), (2) Udvardy's biogeographic provinces (Udvardy 1975), (3) World Wide Fund for Nature) (WWF) ecoregions (Olson et al. 2001a), and (4) the environmental zones of Metzger et al. (2005; hereafter ESE).

The IEMB was produced to define the biogeographical regions mentioned in Art.1 c) (iii) of the Habitats Directive (Figure 2) and is the official geographical framework for which Sites of Community Interest are designated and for monitoring and reporting on habitat types (Article 17 reporting). The IEMB was formally adopted by the Habitats Committee, the body established to oversee the implementation of the Habitats Directive. It is based on interpretations of the "Map of Natural Vegetation of the Member Countries of the European Community and of the Council of Europe" and the "Map of the Natural Vegetation of Europe" (Noirfalse 1987, Bohn et al. 2000, ETC/CB 2006) with each mapping class allocated to a biogeographical region or a group of azonal habitats. The resulting map was then generalized and in some cases adjusted for administrative convenience. The map is also used for the Emerald network, a network of protected areas under the Bern Convention. Since the SWG decided not to define sub-regions but to produce a biogeographic map at a smaller scale (1:10 million), the natural vegetation map needed to be aggregated and generalized. Vegetation classes were allocated to biogeographic regions. In the case an attribution to one particular region was impossible this area was incorporated into neighboring biogeographic regions. The delineation of regions was carried out for the territory of the EU12. The European biogeographic map was further expanded, 1) as more Member States joined the EU and, 2) to provide a biogeographic map of "Pan-Europe" within the framework of the Emerald network. The Emerald network under the Bern convention is a geographical complement of the Natura 2000 network in non-EU countries (see e.g. Tillmann 2005). The expansion of the biogeographic map was generally used by Member States to suggest modifications of border delineations (ETC-BD 2006). Politically induced amendments were carried out e.g. in Germany for the border delineation between Atlantic and Continental, as well as Alpine and Continental regions. Furthermore, Lithuania was placed entirely in the Boreal biogeographic region despite the fact that approximately half of the country is regarded to lie within the Continental biogeographic region.

In the 1960ies, the goal of establishing a worldwide network of natural reserves encompassing representative areas of the world's ecosystems was widely supported (Whittaker et al. 2005; Kleft and Jetz 2010). In this context, the IUCN commissioned the biogeographer Udvardy to develop and refine the method of distinguishing biotic provinces (Udvardy 1969) incorporating Dasmann's (Dasmann 1972,
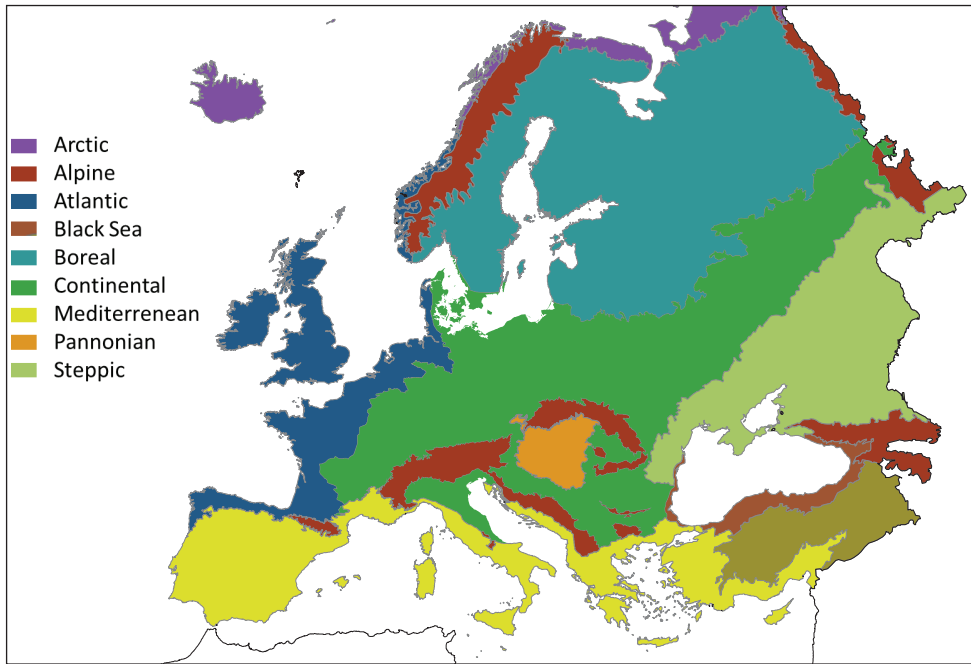
Figure 2. Indicative European Map of Biogeographic Regions (EEA 2006). For further information please see http://ec.europa.eu/environment/nature/natura2000/sites_hab/biogeog_regions/index_en.htm

Dasmann 1974) biotic classifications of faunal regions and vegetation zones (Whittaker et al. 2005; Table 1).

A third map, the WWF ecoregions map (Dinerstein et al. 1995, Olson et al. 2001b; Table 1) was developed since no biodiversity map with a sufficient biogeographic resolution existed to accurately reflect the world's distribution of biotic communities. Ecoregions are defined as relatively large units of land where characteristic species and habitats occur or did occur prior to land use changes. The WWF map of ecoregions was criticized for the lack of scientific explicitness, transparency, and repeatability of methods (Whittaker et al. 2005), and for missing tests of border delineations of ecoregions (Magnusson 2004).

The Environmental Stratification of Europe (hereafter called ESE; Metzger et al. 2005) was generated to produce a statistical stratification of the environment, which is suitable for stratified random sampling of ecological resources and the selection of sites for representative studies. Previous methods to statistically stratify the environment suffered from limitations, such as a coarse resolution or a small area in focus (Metzger et al. 2005), the ESE uses a resolution of 1 km × 1 km and covers Europe as a larger focal area. The stratification was based on twenty environmental variables, examined in earlier studies (see e.g. Bunce et al. 2010). These variables were derived from elevation data acting as surrogates of geomorphologic information, climatic variables, and indicators of northing and oceanity. A statistical clustering led to 84 environmental strata, which can be aggregated into 13 environmental zones (Figure 3; Table 1). The statisti-

Table 1. Comparison of the four biogeographic maps.

	Udvardy's system	Indicative European Map of Biogeographic Regions (IEMB)	Environmental Zones (ESE)	WWF Ecoregions
Development	Developed for the IUCN between 1970-1975 by Dasman and Udvardy (Udvardy 1975)	Scientific Working Group of the Habitats Directive, (ETC-BD 2006)	Metzger et al. (2005)	World Wildlife Fund for Nature, Olsen et al 2001a
Name of regions	Biogeographic provinces	Biogeographic regions	Environmental zones	Ecoregions
Basic principle	Combining ecoclimatic features and taxonomic differences, biogeographic provinces delineated by faunal regions and climax vegetation type	Based on "Map of Natural Vegetation" (Noirfalse 1987) & Map of Natural Vegetation of Europe. Vegetation units were allocated to biogeographical regions followed by generalization & simplification	Climatic stratification of the environment of Europe, based on statistical clustering of environmental variables	Delineations regarding species compositions, ecological dynamics, shared environmental conditions and, ecological interactions
Number of European regions	14	8	13	44
Number of (land) regions relevant for forest habitats	13	7 regions for EU25, 9 for EU27, and 11 for Pan Europe.	12	40
Advantages	Consistent algorithms, not politically influenced	Widely accepted by policy makers	Scientific statistical approach not politically influenced, based directly on climatic variables, not vegetation	Not politically influenced
Weaknesses	Vegetation as determining factor	Border adjusted for administrative convenience vegetation as determining factor		Large number of regions, inconsistent delineation, based on vegetation

cal analysis provides robust divisions based on the combination of variables even in regions where large-scale continuous gradients occur (e.g. Northern Spain). The statistical approach is reproducible and independent of personal bias (Metzger et al. 2005). Currently, the environmental stratification is used for several applications, including as units for summary reporting (Metzger et al. 2008), for estimation of potential areas for cultivation of bio-energy crops, or for prediction of future crop yields (Ewert et al. 2005). The approach is currently being extended to give an environmental stratification of the world (Metzger et al. 2011, in press).

Table 1 summarizes the characteristics, advantages, and disadvantages of the four maps. Vegetation is used as the main determining factor for delineating regions in all
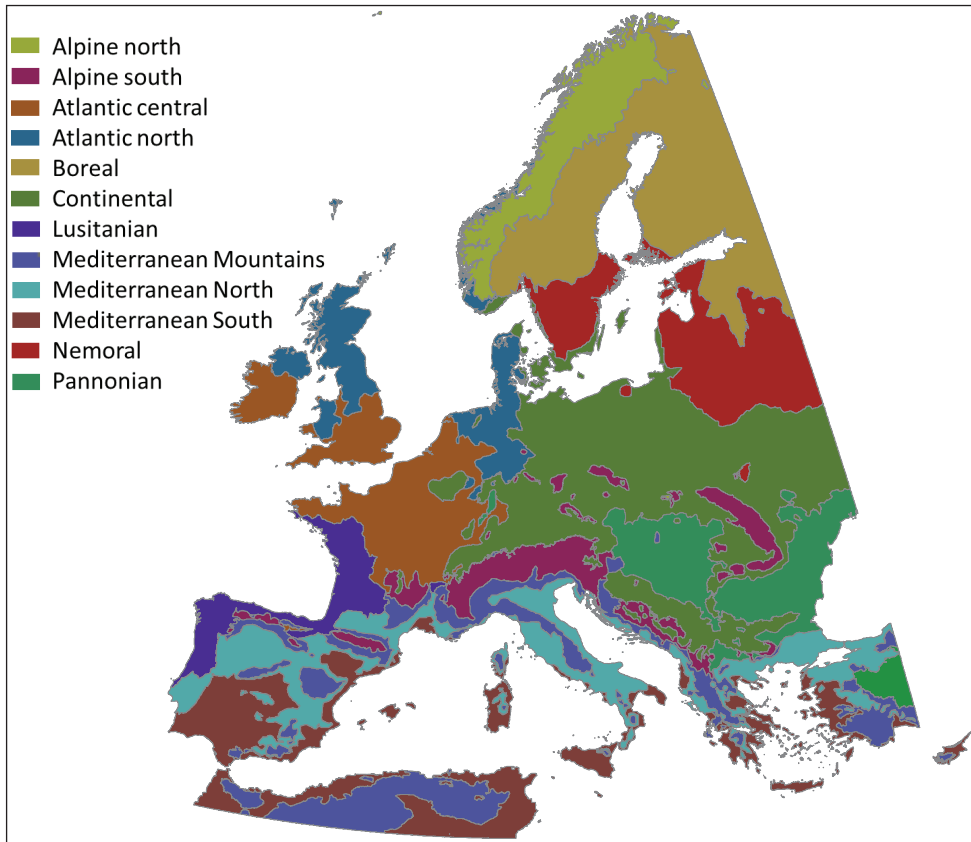
Figure 3. Environmental Zones of Europe (Metzger et al. 2005).

except the environmental stratification zones of Metzger et al. (2005), which is based on climatic factors. The latter is the only map that is founded on a statistically rigorous stratification though Udvardy's map also uses a consistent algorithm to delineate regions. In the IEMB borders of regions were adjusted due to requests of Member States to reduce the administrative load, thus not always using environmentally consistent borders. However, it has the advantage that it is widely accepted politically. It also has the coarsest resolution, whereas the WWF ecoregions recognize the largest number of different regions within Europe (see Table 1 for details). A comparison of the different maps (see Annex Table A1-3), shows marked differences between them. For most zones the correspondence among the four maps is limited (often less than 75%).

Distribution pattern and the different biogeographic and environmental maps

Comparison of the different biogeographic maps has shown differences between each of them, e.g. the number of biogeographic regions or environmental zones is not the same. Thus, habitats may occur in more zones when using fine-grained biographic

zones than when using coarser grained maps. Moreover, as environments rarely have abrupt natural borders, any stratification will sometimes allocate similar environments on both sides of a border into different categories. This can result in habitats with small distributions occurring in 2 or more zones. For example, habitat 91R0, "Dinaric dolomite Scot's pine forest (*Genisto januenis-Pinetum*)", with a reported distribution area of 2885 km^2 belongs to the 10 habitats with the smallest distribution ranges but is found in two zones of the IEMB map. The definition of classes of the distribution pattern used should reflect these aspects in such a way that the distribution of habitats across responsibility classes should not deviate too strongly from each other when different biogeographic concepts are used and should not allocate habitats with a small distribution area into a wide category. Here, we develop the categories for two maps, the ESE, as it has been widely accepted in habitat monitoring and is based on objective criteria for the delimitation of the different environmental zones, and the IEMB map, which has a legal status.

For the IEMB map, a **local** distribution pattern is attributed to habitats occurring in patches belonging to a single biogeographic region. **Regional** are habitats with a up to two-thirds of the distribution area in one biogeographic region. **Wide** refers to habitats with a distribution spanning two or more biogeographic regions.

For the ESE, a **local** distribution pattern is attributed to habitats occurring in only one environmental zone. Habitats have a **regional** distribution, if they are restricted to two neighboring environmental zones. All habitats with a distribution spanning three or more environmental zones were considered habitats with a **wide** distribution.

Step 3: Expected distribution probability

The third step of the proposed national responsibility method is to determine the expected value of occurrence (OV_{exp}) in the focal area (e.g. a country). Following the suggestion of Keller and Bollmann (2001, 2004), first the expected distribution probability (DP_{exp}) and the observed distribution probability (DP_{obs}) are compared. DP_{exp} is calculated as the ratio of the total distribution area of the habitat and the size of the reference area, while DP_{obs} is obtained as the ratio of the distribution range of the habitat in a focal region (country) to the total size of the focal region. If the latter value is above double the expected distribution probability, the expected value of occurrence of a habitat in the focal area is high, whereas below it is classified as being low ($DP_{obs} > 2*$ DP_{exp} Þ OV_{exp} = High; $DP_{obs} < 2* DP_{exp}$ Þ OV_{exp} = Low).

The reference area should comprise the potential distribution area of a habitat in order to correctly determine whether the habitat distribution within a focal country plays a crucial role for the global persistence of a habitat or not. The main difficulty with this approach is data availability on habitat distribution and the different definitions, which exist world-wide. Also, different habitats will have different distributional limits so that whatever the reference area is some habitats will be included only incompletely or marginally. Several reference areas might be considered appropriate

for European habitat types, 1) geographical Europe (Ural as eastern border; extent 10.936.779 km²), 2) the Western Palearctic (Europe, the Middle East, and North Africa, 33.225.342 km²), or 3) the Palearctic (including Europe, northern Africa, Russia, northern and central Asia, covering 54.244.453 km², see Kreft and Jetz 2010 for other potential reference areas outside of a European context).

Another important decision in this last step concerns the cut-off value. When can we consider an observed distribution probability as high or low? If the observed probability is twice as high as the expected value does this count as high? Given that the Agenda 2010 and the Aichi targets oblige European Member States to conserve a significant part of its biodiversity in each biogeographic region, this third and last step, as suggested here, should be conservative and accounts for the international importance of a habitat in a country and within a biogeographic region.

National responsibilities for EU forest habitats

As a test of the proposed methodology, we determined national responsibilities across geographical Europe, the Western Palearctic region, and the Palearctic region as reference areas and the ESE and IEMB maps for the 71 Annex I forest habitat types occurring in the EU25 (Table A4). We assessed national responsibilities using spatial datasets giving distribution of the habitats (EEA 2009). The habitat distribution across biogeographic regions of both biogeographic maps was created by overlaying shapefiles with a biogeographic map using the "Identify" tool from the "Analysis tools" in ArcGIS v10 (Esri), which attributes names of the biogeographic regions to the habitat distribution polygons. Polygons stretching over several regions were cut at biogeographic borders and each new polygon was attributed the name of the underlying region. Afterwards, we calculated the area of the habitat distribution polygon for the biogeographic region(s) where it occurred.

Results

The highest number of forest habitat types was found in Italy (36 out of 71; 51%) followed by France (29, 41%), Spain (28, 39%) and Greece (27, 38%; Figure 4). The number of habitat types was positively correlated with the size of the country (R_{23} = 0.702; $p < 0.001$).

The distributions of natural responsibility (NR) classes largely resembled each other for the different combinations of reference area and biogeographic map. The most common rank in all cases was "medium"; the rank "very high" was the least common (Figure 5). We compared the number of NR-ranks of the six different combinations of reference area and biogeographic map using the combination Europe as reference area and the IEMB map as a baseline. The least affected rank in all the different assessments was the rank "very high", which showed an N between 22 and 24. The largest differences were found for the "basic" rank. The number of this rank ranged between 59 and 134 (Figure 5). With increasing size of the reference area, a shift from allocations to a basic rank to allocations to a medium rank (from 1:4 to 1:1) was observed (Figure 6;
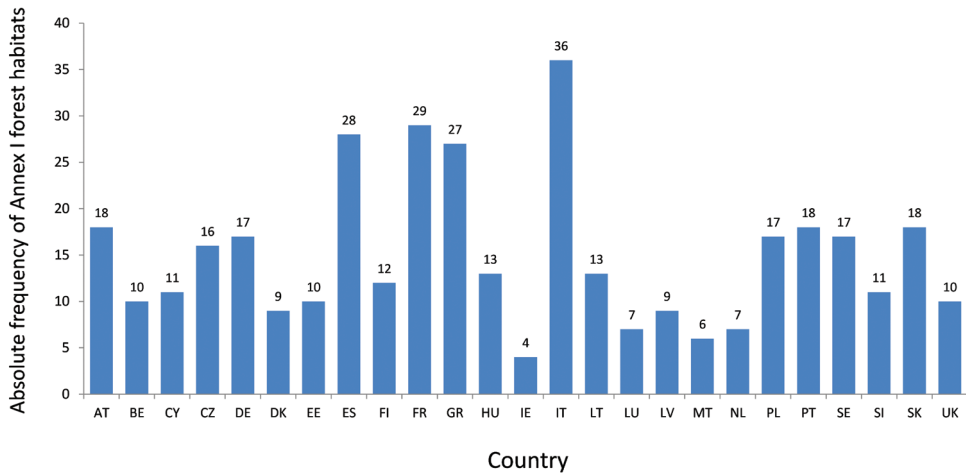
Figure 4. Number of forest habitat types as defined in the Annex I of the Habitats Directive by European country. The countries are abbreviated following the two-letter convention of the international community (ISO 3166-1 alpha-2 codes; **AT** = Austria, **BE** = Belgium, **CY** = Cyprus, **CZ** = Czech Republic, **DE** = Germany, **DK** = Denmark, **EE** = Estonia, **ES** = Spain, **FI** = Finland, **FR** = France, **GR** = Greece, **HU** = Hungary, **IE** = Ireland, **IT** = Italy, **LT** = Lithuania, **LU** = Luxembourg, **LV** = Latvia, **MT** = Malta, **NL** = Netherlands, **PL** = Poland, **PT** = Portugal, **SE** = Sweden, **SI** = Slovenia, **SK** = Slovakia, **UK** = Great Britain).
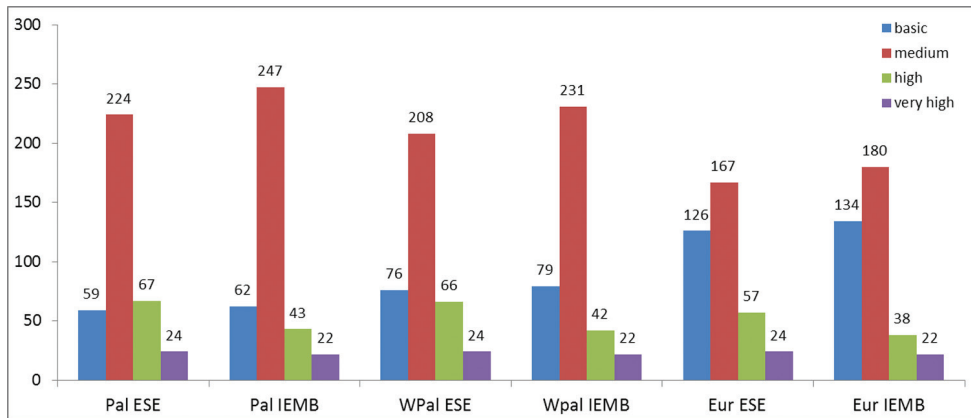
Figure 5. Distribution of National Responsibility ranks in the different combinations of reference area and biogeographic map. Reference area: **Pal** = Palearctis, **WPal** = Western Palearctis, **Eur** = geographic Europe; maps: **ESE** = Environmental zones, **IEMB** = IEMB biogeographic map.

Figure 7). The comparison of the allocation of habitats to responsibility classes between the two different biogeographic maps ESE and IEMB showed a shift from lower to higher ranks for all three reference areas, especially a shift from the ranks "medium" toward "high" (Figure 7), for the finer grained ESE map.

Comparing the two biogeographic maps by country reveals shifts mainly from medium to high ranks for northern countries (EE, LV, LT, FI, SE) and countries in the
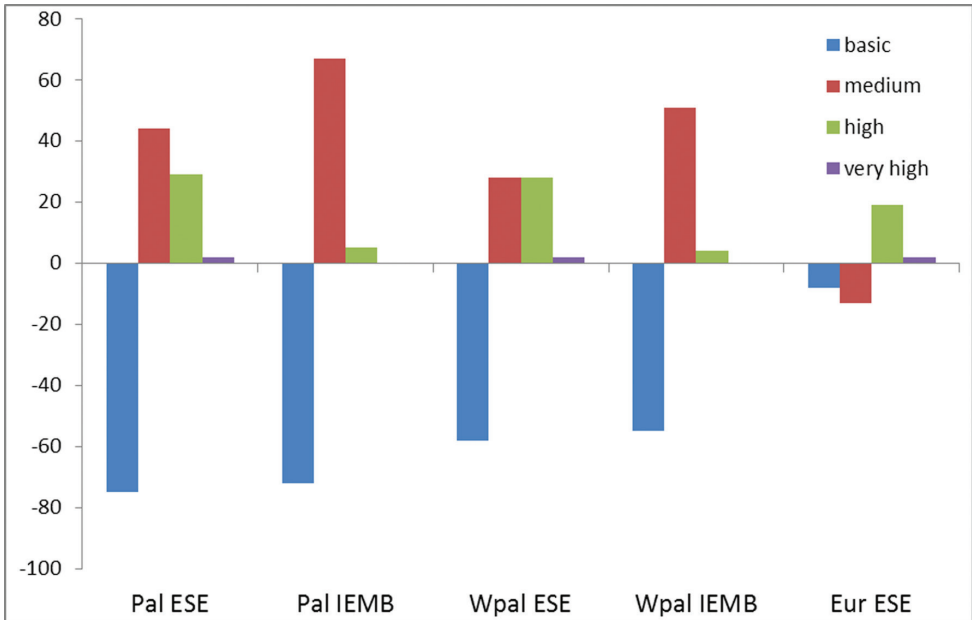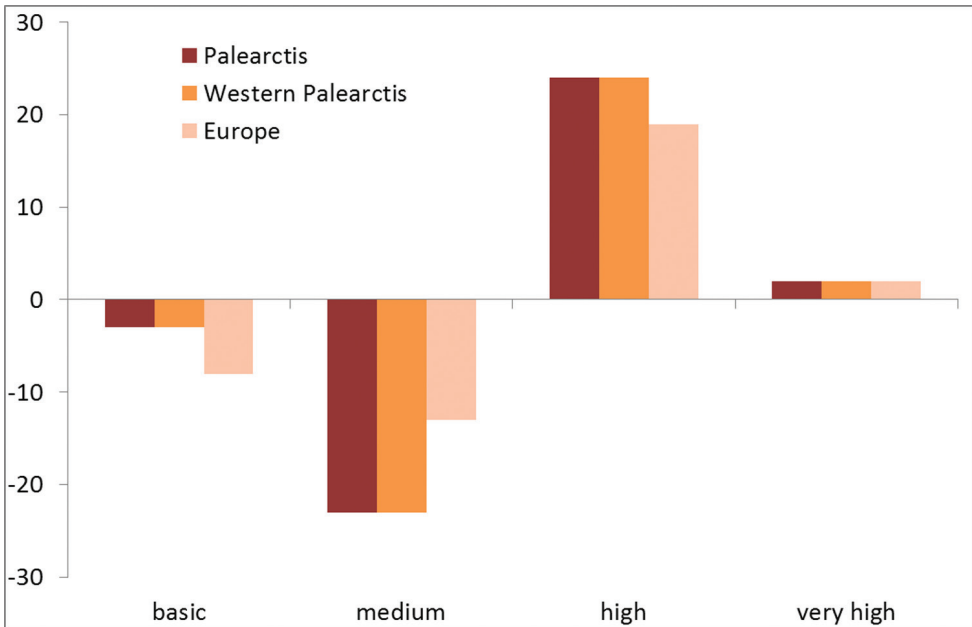
Figure 6. Differences in the National Responsibility-rank distribution between the assessments with Europe as reference area and the IEMB biogeographic map and the other 5 combinations (reference area: **Pal**= Palearctis, **WPal** = Western Palearctis, **Eur** = geographic Europe; maps: **ESE** = Environmental zones, **IEMB** = IEMB biogeographic map).
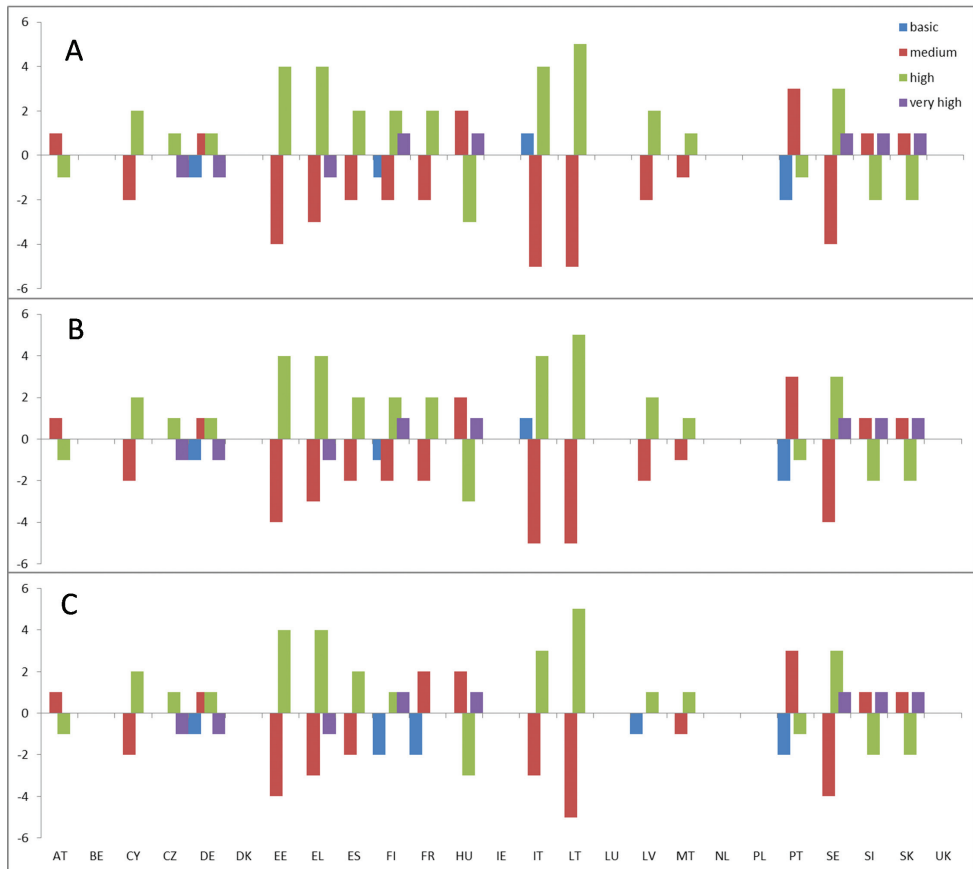

Figure 7. Shifts of the allocation of forest habitat types to responsibility classes when using the ESE versus the IEMB within each reference area.

Mediterranean bioregion (ES, IT, FR, CY, PT). Changes were the least for countries in Central and Western Europe (BE, IE, LU, NL, PL, UK; Figure 8). We also found higher ranks with increasing size of the reference area (comparison of Palearctic Region to geographical Europe in Figure 9). The strongest shifts from basic to medium ranks were observed for AT, DK, FR, and IT.

A multiple regression of the differences in the rank "medium" between NR assessments based on the ESE map using as reference area the Palearctic region or geographical Europe ($F_{2,22}$ = 6.899; p = 0.005) showed a difference, but this difference was not explained by the size of a country (t_{22} = -1.304; p = 0.205). Differences were mainly driven by the number of habitats occurring within a country (t_{22} = 3.507; p = 0.002).

Figure 8. Shifts of the allocation of forest habitat types to responsibility classes per country when using the ESE versus the IEMB biogeographic map for the different reference areas: **A**=Palearctis; **B** = Western Palearctis; and **C** = Europe. The countries are abbreviated following the two-letter convention of the international community (ISO 3166-1 alpha-2 codes; **AT** = Austria, **BE** = Belgium, **CY** = Cyprus, **CZ** = Czech Republic, **DE** = Germany, **DK** = Denmark, **EE** = Estonia, **ES** = Spain, **FI** = Finland, **FR** = France, **GR** = Greece, **HU** = Hungary, **IE** = Ireland, **IT** = Italy, **LT** = Lithuania, **LU** = Luxembourg, **LV** = Latvia, **MT** = Malta, **NL** = Netherlands, **PL** = Poland, **PT** = Portugal, **SE** = Sweden, **SI** = Slovenia, **SK** = Slovakia, **UK** = Great Britain).
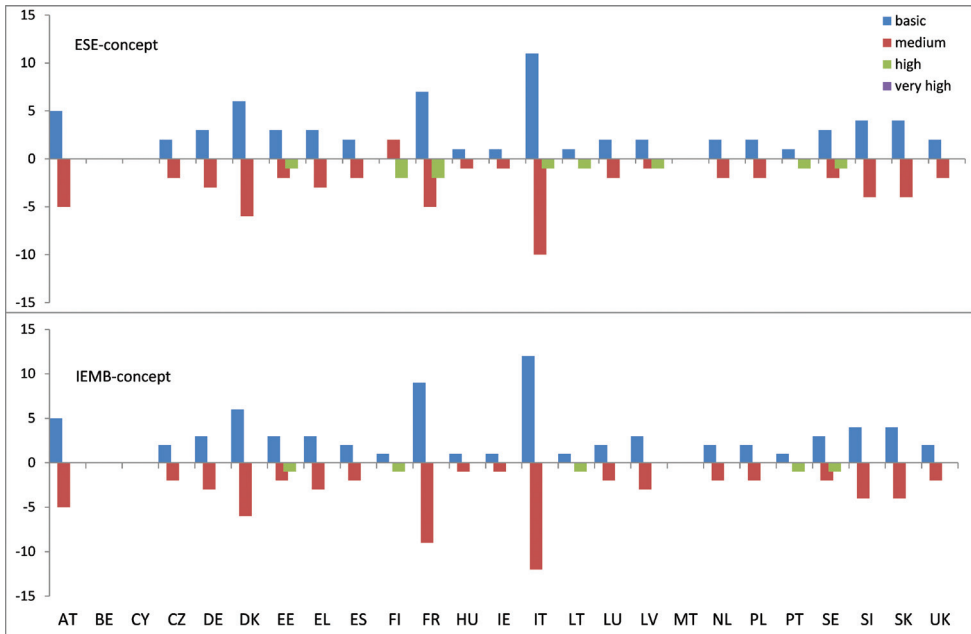
Figure 9. Shifts of allocations to ranks of national responsibility classes of countries when using the Palearctic versus Europe as reference area for the ESE and IEMB-maps. The countries are abbreviated following the two-letter convention of the international community (ISO 3166-1 alpha-2 codes; **AT** = Austria, **BE** = Belgium, **CY** = Cyprus, **CZ** = Czech Republic, **DE** = Germany, **DK** = Denmark, **EE** = Estonia, **ES** = Spain, **FI** = Finland, **FR** = France, **GR** = Greece, **HU** = Hungary, **IE** = Ireland, **IT** = Italy, **LT** = Lithuania, **LU** = Luxembourg, **LV** = Latvia, **MT** = Malta, **NL** = Netherlands, **PL** = Poland, **PT** = Portugal, **SE** = Sweden, **SI** = Slovenia, **SK** = Slovakia, **UK** = Great Britain).

Discussion

In the light of continuing decline of natural habitats (CBD 2010) and on-going biodiversity loss (Ricketts et al. 2005, Hoffmann et al. 2010), the commitment for nature protection legally defined in the Birds and Habitats Directives requires urgent implementation. As resources remain scarce, states are forced to determine their national responsibilities and set conservation priorities. Here we propose a method to determine national responsibilities for European habitat types, following a methodology initially developed for species (Schmeller et al. 2008b). The method was applied to 71 forest habitat types using three different reference areas and two different biogeographical maps. We found a shift to higher national responsibility ranks with increasing size of the reference area, due to an increasingly smaller ratio between reference area and total distribution area. We also observed a shift from medium to high national responsibility ranks when using the finer grained ESE (Metzger et al. 2005), as compared to the IEMB map. However, the lowest ("basic") and the highest rank ("very high") were little changed by the choice of biogeographical/environmental map. Further, our method was not directly influenced by the size of a country, but rather by the number of habitat types found within each country.

The method proposed here, while scientifically sound and relatively robust, suffers from two main issues related to the conservation of habitat types, 1) the lack of a globally and even regionally accepted habitat classification, and 2) the limited availability of distribution data across biomes, such as the Western Palearctic or the Palearctic in general. The first point impacts on the method in two ways, firstly, it restricts its usability to habitats with the same definition standard, and secondly comparability of national responsibilities of habitats with the same definition may not be totally correct, as important elements can differ in habitat types found e.g. in northern or central Europe due to environmental or ecological drift (e.g. Ewald 2003). In addition, differing habitat definitions make it cumbersome to retrieve information on the total distribution area of a habitat type as well as it does impact on the monitoring of a habitat type *per se* (e.g. Mücher et al. 2009). If a habitat definition is unclear, monitoring data from different sources (e.g. national authorities responsible for nature conservation) may not be compatible. Further, if the same habitat has different names in the European Union than e.g. in Russia, the total distribution area is difficult to determine. From a conservation perspective, our method would overestimate the responsibilities for a habitat type in case we underestimate its complete distribution area or in case a habitat type definition has created a subtype of a habitat (hence it would be likely small and patchy). Hence, we consider our proposed method as conservative and thus applicable, at least to the European situation.

The aim of our method, however, is to create a globally applicable method to determine national responsibilities. Accepted habitat classifications and spatial information on their distribution are therefore urgently needed, as recommended in a recent article (Rodríguez et al. 2011). Once such data are available, we recommend the following addition to our methodology: A first biome-wide assessment of the distribution probability needs to be undertaken, comparing the expected and observed distribution probability of a habitat e.g. for Europe, the Middle East, and Asia. If the distribution probability is high, a finer scale assessment, with a reduced reference area (for habitats in Europe currently geographical Europe might be the best) needs to be done. This way, habitat types can be partitioned out between e.g. Europe, the Middle East and Asia, avoiding doing assessments of habitats with a very small part of their global distribution in the focal area.

In conclusion, the methodology to determine national responsibilities presented here is readily applicable to determine conservation responsibilities for habitats of the EU25 countries. It should be based on the environmental stratification of Europe (ESE; Metzger et al. 2005) and should use geographical Europe as the reference area due to limited data availability outside of Europe. For a fully comprehensive coverage of conservation needs, the national responsibilities for both species and habitats would need to be determined. Our method then provides a tool to allocate funds, direct conservation actions in the most sensible way, and point out data gaps (currently mainly the EU). Currently, distribution data is only available for the habitats of Annex I of the Habitats Directive but this is not based on a single habitat classification and the habitats are drawn from varying levels. Annex I also includes both habitat types and landscape units. Poor definitions and overlapping habitat types lead to frequent misinterpretations and data coherence needs to be improved to obtain a unified, logical

and science-based classification of habitats for Europe and globally (see also Davies et al. 2004, ETC/BD 2008). Only with such a classification and distribution data will it be possible to determine national responsibilities for all habitat groups; the higher the standardization of the habitat classification and the quality of the (distribution) data, the higher the accuracy and reliability of the assessment. Generally, national responsibilities can be estimated based on any biogeographical map, although, due to politically influenced delineation of regions, small number of biogeographic regions, and interrelations with the chosen habitat classification, the application of the IEMB map leads to overall lower national responsibilities than the use of other maps. We do not consider this as an important problem, as the order of habitats in the priority list obtained by our methodology only changed in very few cases and because the two highest responsibility classes were rather robust to changes in the biogeographic map.

There are two more important problems, which need to be considered in the future, 1) the variability in the quality of a habitat and 2) the coherence of distribution data. The quality of a habitat type has not been homogeneously assessed across Europe, but may depend on management history, size, pollution and other factors. Our method can capture habitat quality by replacing the step on distribution pattern (as also suggested for the species method using abundance data) with a quality index. However, such data is not available widely and thus currently not applicable. Secondly, in the future, coherent distribution data, based on a consistent and complete habitat classification, should be gathered and made available across more countries than the EU25. Then, the methodology to determine national responsibilities has a unique potential to set, in combination with existing systems of threatenedness, such as Red Lists, conservation priorities (Schmeller et al. 2008a). It can contribute to effectively close gaps in habitat protection networks and prevent the further decline of natural habitat types, also beyond the European Union borders and would also emphasize the concept of biodiversity hotspots, while not ignoring habitats and species that do not occur in hotspots (Ernst et al. 2000).

Acknowledgements

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Appendix

Supplementary information to National responsibilities for conserving habitats - a freely scalable method. (doi: 10.3897/natureconservation.3.3710.app). File format: MS Word Document (docx).

Explanation note: The annex does provide a more detailed comparison of the different biogeographic maps. It further gives a list of all forest habitats given in the EU Habitats Direction.

RESEARCH ARTICLE

"Mind the gap!" – How well does Natura 2000 cover species of European interest?

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Abstract

Setting aside protected areas is widely recognized as one of the most effective measures to prevent species from extinction. Accordingly, there has been a tremendous effort by governments worldwide to establish protected areas, resulting in over 100,000 sites, which are set aside, to achieve the 10% target proposed at the Fourth World Park Congress in 1992 in Caracas. The main effort of the European Union to achieve this target is the Natura 2000 network of protected areas, comprising over 25,000 sites representing 18% of the area of the 27 Member States of the European Union. The designation of Natura 2000 sites was based on species and habitats listed in the Annexes of the Habitats and Birds Directive. The effectiveness of the selection process and the resulting Natura 2000 network has often been questioned as each country made its designations largely independently and in most cases without considering the theories of optimal

reserve site selection. However, the effectiveness of the selection process and the Natura 2000 network has never been explicitly analysed at the European scale. Here we present such an analysis focusing on the representation of Annex II species of the Habitats Directive in the Natura 2000 network relative to a random allocation of species to sites. Our results show that the network is effective in covering target species and minimizing the number of gap species (i.e. species not represented in a single site of the Natura 2000 network). We demonstrate that the representation is uneven among species. Some species are over-represented and many species are only represented in a low number of sites. We show that this is mainly due to differing patterns in species ranges, as wide-spread species are inevitably represented in many sites, but narrow ranged species are often covered only by a small number of sites in a particular area. Finally, we propose a representation index that detects species that are underrepresented and could be used to direct future conservation efforts.

Introduction

Systematic approaches in planning reserve networks have been intensively developed to guide efficient reserve site selection (Brooks et al. 2006; Drechsler 2005; Margules and Pressey 2000; Margules and Sarkar 2007; Moilanen and Wintle 2006; Myers et al. 2000; Trakhtenbrot and Kadmon 2006). On a global scale no concerted action plan exists to nominate conservation areas, despite repeated calls for international coordination (Brooks et al. 2006; Knight et al. 2007; Mace et al. 2000) and available tools for conservation prioritization (Moilanen et al. 2009; Schmeller et al. 2008b). The main common strategy has been to designate conservation areas for species listed as threatened – so called "Red List species" (Rodrigues et al. 2004a). This encompasses designating those conservation areas where a species occurs, regardless of protection effort in other countries. Although this strategy is generally sufficient to achieve a single representation of each species (but see Rodrigues et al. 2004b), it easily leads to a biased representation of many species. For example, species with a wider distribution range are more likely to be included than species with more confined ranges. In countries of the European Union, a huge effort has been undertaken in recent years to establish and enhance the European Network of protected sites (known as Natura 2000) by designating areas to protect species and habitats listed in the corresponding Annexes of the Habitats Directive and Birds Directive (European Commission 2006).

The effectiveness of the site designation process and the resulting Natura 2000 network has often been questioned (Apostolopoulou and Pantis 2009; Pullin et al. 2009; Sánchez-Fernández et al. 2008). First, the principles of site designation were not uniform and each country selected sites largely independently of other countries (Apostolopoulou and Pantis 2009). Second, explicit criteria and methods of systematic conservation planning (Margules and Pressey 2000; Margules and Sarkar 2007) have rarely, if ever, been applied. A detailed description on the various stages of the designation process has recently been published (Evans 2012). Finally, the perception of the

conservation status of species differs among countries, for example, a species of European importance may be common and perceived as less important for site designation in some countries, whereas it may be considered very important in countries where it is rarer. Such differences may have resulted in different levels of representation of the species in the network, e.g. many designated sites for the species in countries where it is rare and fewer sites in countries where it is common. Even though these and other potential problems have been addressed at a regional scale in a series of "Biogeographical Seminars", which reviewed national proposals for site designations, there has been no systematic pan-European evaluation of the effectiveness of the Natura 2000 network although there have been a number of regional studies , e.g. Greece, Crete, Spain, Poland, and Italy (Araujo et al. 2007; Dimitrakopoulos et al. 2004; Grodzinska-Jurczak and Cent 2011; Iojă et al. 2010; Maiorano et al. 2007) or certain habitat types, e.g. wetlands (Jantke et al. 2010). In these seminars, the site proposals were evaluated, species by species and habitat by habitat, and Member States asked to propose additional sites where judged necessary (Evans 2012).

Here we provide an evaluation of the effectiveness of the Natura 2000 network by studying the representation of Annex species in the non-marine part of the network. In addition, we study the effect of species ranges on representation. We used species range as reported by the Member States fulfilling their reporting requirements under Article 17 of the Habitats Directive (European Commission 2009). Reports were available for all species listed in the annexes of the directive for the period between 2001 - 2006 in Natura 2000 sites from 25 of the 27 current EU member states (Romania and Bulgaria joined after the reporting period and were not included). Species ranges were reported by Member States in a variety of formats but have been standardised to presence/absence on a 10 × 10 km grid by the European Topic Centre on Biological Diversity (ETC/BC) (European Topic Centre on Biological Diversity 2009a).

In 2009 there were 912 species listed in Annex II of the Habitats Directive, which lists threatened species that are to be protected by protected areas (Sites of Community Importance – SCI) in the European Union. Complete range data in a digitized format were only reported for 719 species. The reports do not cover bird species (birds are the subject of the 1979 Birds Directive and not covered by the Habitats Directive), therefore we did not analyse this species group, though in principle our analysis should be possible for this group as well. Finally, our analysis was restricted to a sub-sample of 714 species, where complete distribution ranges were available (see Table S2). For each of these species we extracted the numbers of occurrences (representations) in all Natura 2000 sites that are designated under the Habitats Directive, neglecting areas that are designated due to the Birds Directive, from the June 2009 version of the Natura 2000 database (15,646 sites). Then we compared the representation of these species to the representation that would be achieved by a random allocation of species to sites, to study the effectiveness of the designation process. Once the overall performance was evaluated, we analysed the relationship of representation to a species' range to test if the representation can be primarily explained by species' ranges. Following from this, we created a representation index that is able to detect underrepresented

species to guide future conservation efforts. The Natura 2000 database was provided by the European Environmental Agency for use in the "EuMon" project, a large-scale integrative research project supported by the 6th Framework Programme 6 of the European Union (http://eumon.ckff.si, Henle et al. 2010).

Methods

Gap species

If an Annex II species is not represented at all in the Natura 2000 sites, it is termed a gap species (sensu Rodrigues et al. 2004a). There are numerous ways to identify gap species in a reserve network, which depend on different sources of data. The most common approach is a GIS-based approach to overlay species range data onto a map of protected areas. In this kind of analysis a species is regarded as represented in a protected area if its range falls at least partly within it (Kremen et al. 2008; Rodrigues et al. 2004a; Rodrigues et al. 2004b). Often an arbitrary threshold, such as 10 % of the area, has to be covered before a reserve network is assumed to assure a species is efficiently protected. Given that species range maps are often highly erroneous due to incomplete and outdated data, this approach is problematic, especially for rare species (Rodrigues et al. 2004b). It is even more problematic if species ranges are given by occurrences in grid cells, as is the case here. In that case, an additional assumption has to be made: if a site of a network falls inside a grid cell where the species is present, the species is represented. Often this results in commission errors, i.e., a species is considered to be present in a protected area when it is absent (Rodrigues et al. 2004a). To avoid these potential errors we used the Natura 2000 database, which describes each Natura 2000 site and lists the Annex II species present, often based on recent ecological surveys in the protected areas. To identify gap species we queried the data base for how often a species occurred across all sites. Species without any entries were regarded as gap species.

The Natura 2000 database is constantly being updated due to additional designation of sites and changes to the description of existing sites, including the addition or deletion of Annex II species. However, poor data entry, such as misspelt species names, also introduces errors and, although the data are checked regularly, it takes time for Member States to make the corrections. Each of these effects may result in erroneous entries in the database, which in turn can lead to an under-estimation of representation and to a surplus of gap species. This may result in a higher number of so called omission errors (a species is considered to be absent from a protected area in which it is present). We believe our more conservative, precautionary approach is a more appropriate one for nature conservation, as a species that is falsely regarded underrepresented is less problematic than a species falsely regarded as overrepresented, which could potentially lead to the misguided believe that the species is adequately protected. As the database is continuously updated, we decided to use the database after the last reporting in 2009 to have a fixed reference status for future comparisons.

Selection process

To assess the efficiency of the designation process, we simulated a random designation process by assigning 714 species into 15,646 virtual Natura 2000 sites assuming that the probability of drawing a species is the ratio of its range size to the total area of the EU25 Member States. This designation process was virtually repeated 1000 times using a Monte Carlo approach, during which the distribution of representations of the 714 species was recorded for each random sample. Based on these thousand samples a confidence interval of the expected number of representation for each representation class can be created. If the distribution of observed representation is not following the distribution of representation of the random process (i.e. is above or below the 95% confidence interval), this suggests departure from a non-random and hence "organized" designation process.

Representation and range size

To analyse if the representation of a species is mainly determined by its range size we regressed these two variables against each other. Given this relationship, we wanted to quantify the status of representation of each species, i.e. whether it is overrepresented or underrepresented, taking its range size into account. Therefore we devised a representation index (REX). To calculate this index for each species, we first determined the range size of each species by summing the occurrences in grid cells of 10 x 10 km extent and multiply this by the area of one cell (100 km²). We standardized this range size by dividing it by the total area of all EU25 countries, which results in a range size proportion between zero and one. Then we calculated the representation proportion for each species by dividing the representation of each species by the total number of Natura 2000 sites in the EU25 countries. Finally, the REX is calculated as the ratio of these two quantities:

$$REX = \frac{\text{representation proportion}}{\text{range size proportion}} = \frac{\dfrac{\text{representation}}{\text{number of Natura 2000 sites in EU25}}}{\dfrac{\text{range size}}{\text{total area of EU25}}}$$

The index can be calculated for the whole of the Natura 2000 network, as well as for subunits of the network (either per country or per species group). To compare the REX among groups of species we used the median of each species per group to down weight outliers. In addition, the median REX of all species in a country can be used to compare the status of representation of all species among countries, as it can be standardized by taking the country area and number of Natura 2000 sites in a country instead of the EU25 area and number of sites as a reference.

The idea of the REX is best illustrated by an example. Assume a species whose range covers 50% of the area of the EU25 countries. If this species is represented in half of the Natura 2000 sites of the EU25 countries, it has a REX value of one, since it is represented in accordance to its range. If the species is represented in more than 50% of the sites, the REX value would be larger than one, showing an overrepresentation of

a species. A REX value below one indicates an underrepresented species. A REX of two means that this species is twice as often represented as would be expected from its range size. Obviously, the higher the REX the better a species is represented and therefore its conservation is more likely to be adequate.

Results

Representation

Of the 714 species examined, 54 were apparently not recorded in any site (Fig. 1). Checking each gap species separately, most of the zero representations are due to incomplete data in the database. Most often the incompleteness of data results, either from 'confidential species', where data has deliberately been excluded from the database, or due to taxonomic changes. We had a closer look on the identity of gap species in the database. Together with experts from the ETC/BD, we created a complete list of gap species and comment on their likely status (Table S1). Among the species studied we identified three genuine gap species and these were already identified by "Biogeographical Seminars" (Papp and Toth 2006). Most of the other identified gap species are the result of incomplete reporting. Nevertheless, as a first result, the analysis of the representation of each species pointed towards potentially erroneous entries and real gap species. Notwithstanding, while not as problematic for the design of further conservation activities, such as the search for additional appropriate sites for protection, lack of information may also hamper the effectiveness of further action. In addition, the uneven distribution of representations clearly demonstrates that the selection process strongly favoured some species represented in many sites and lead to a representation of many species in a low number of sites.

Selection process

The resulting distribution of simulated random representations showed a very good fit with observed data (Kolmogorov-Smirnov-Test, D = 0.22, p>0.765), except for gap species, where the observed representation showed significant lower values, and for single plus double representations, which had significant higher values in the observed data (Fig. 1). This demonstrates that the designation process was highly effective in avoiding gap species, as it shifted them to single or few representations, but at higher representations the outcome of the designation process conforms to a random pattern.

Comparing representation and range size

Species representation is highly correlated with species range size (Fig. 2, $F_{1, 712}$ = 1274.3, P < 0.0001, r = 0.81). Most species are scattered around the bisecting line,
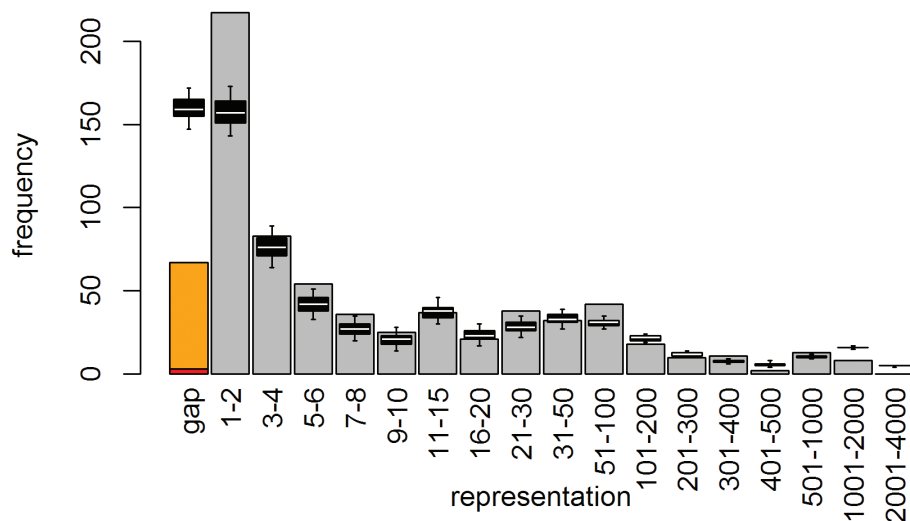
Figure 1. EU-wide representation of 714 Annex II species in the Natura 2000 network of the EU25 countries of the European Union in 2007. Species with no representation in the data base, (gap species: 54 / 714) are indicated by an orange bar. Remaining gap species based on expert knowledge are marked by the red bar (3 / 714). Whisker-boxes show the distribution under random assignment, assuming that the probability of a species to be assigned is proportional to the range size of that species. White lines indicate the median, boxes the first and third quartiles and whiskers the 5 and 95 percentile of 1000 replicates.

which can be interpreted as a null model for representation. Gap species occur from very small range sizes (likely real gap species) up to ranges of more than 30,000 km² (probably gap species due to incomplete entries). The representation index (REX) has a median value of 3.17 over all species for the Natura 2000 network of the EU25. This indicates that most species are represented three times more than would be expected from the species range. Of all 714 species 599 had a REX value higher than 1, so the majority of species were overrepresented in the network (Table S2).

For demonstration purpose we will elaborate on the REX using four exemplary species. These species show the four principally combination of distribution and representation, namely broad/narrow ranged species, which are over/under represented (Table 1).

Myotis bechsteinii (wide range/ low representation)

The Bechstein's bat (*Myotis bechsteinii*) is a representative of the case where a species is widely distributed across Europe, but because it is specialised on a nowadays rare habitat - mature deciduous forests - it is only recorded in 27 sites across its range. The EU assessment of the species (European Topic Center 2009b, Report on *Myotis bechsteinii*) shows that in many countries and biogeographic regions the conservation status of *Myotis bechsteinii* is unknown, due to its highly cryptic nature. It has a very low REX value (0.04) which is in line with the current known representation of the species. An obvious recommendation would be to increase the knowledge on the actual distribu-
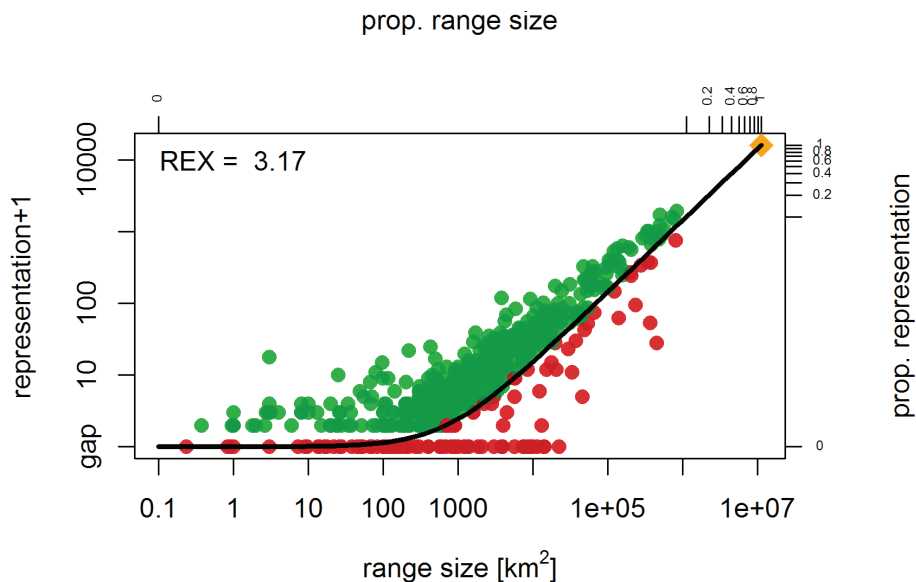
Figure 2. The relationship between species representation and range size for 714 Annex II species in the EU25 countries. Red dots indicate underrepresented species (REX < 1) and green dots overrepresented species (REX > 1). The bisecting line marks values of REX equal to one. Note that the bisecting line turns into a curve on a log-log scale. The orange diamond marks the maximum possible representations for a hypothetical species distributed over the total area of the EU25 countries. The median representative index for all species is given in the upper left corner.

Table 1. Example of representation, distribution and REX of four species.

Species	Representation [number of N2K sites]	Distribution [km²]	REX
Myotis bechsteinii	27	452395	0.04
Paracaloptenus caloptenoides	4	4588	0.06
Mustela lutreola	119	3802	21.83
Lutra lutra	3185	1382075	1.61

tion of the species, which hopefully leads to the identification of additional Natura 2000 sites that already protect a population of the species, followed by potential new designated sites to increase the overall representation.

Paracaloptenus caloptenoides (narrow range / low representation)

The cricket *Paracaloptenus caloptenoides* is an endemic, narrow-ranged species that occurs mainly in Hungary, with some population reported from Slovakia and Greece. In its limited range it is only represented in four Natura 2000 sites, which results in a very low REX value (0.06). Based on the assessment of the EU (European Topic Centre 2009b, Report

on *Paracaloptenus caloptenoides*) it is regarded to be overall in an unfavourable status as there is a lack of knowledge on the distribution of the species (Slovakia and Greece) and the status in Hungary is critical. Therefore we conclude that the low REX value is in line with the current knowledge on the species and its representation in Natura 2000 sites.

Mustela lutreola (narrow range / high representation)

The European Mink (*Mustela lutreola*) is an example of a species that has a very limited current range, probably due to destruction of habitat and replacement by the invasion of the American Mink (*Neovision vision*) in Europe. The remaining current distribution is therefore very fragmented and scattered across Europe (European Topic Centre 2009b, Report on *Mustela lutreola*). Being critically endangered, this species has received considerable attention and is currently represented in 119 sites. This leads to a very high REX value (21.8). Therefore we conclude that the species is well represented by the Natura2000 network, but as the population is still in decline, management should concentrate on restoring the habitat and controlling the American mink at sites where both species occur.

Lutra lutra (wide range / high representation)

The Eurasian otter (*Lutra lutra*) is a widespread species that is represented in more than 3000 sites and has therefore an overall REX value of 1.6. This demonstrates that the species is well covered by the Natura2000 network and the REX is in line with its status based on the EU assessment (European Topic Centre 2009b, Report on *Lutra lutra*). While its conservation status may be insufficient in some biogeographic regions, it is "*favourable in a number of countries with stable or increasing trends and good future prospects*" (European Topic Center 2009b, Report on *Lutra lutra*).

To summarize the examples, it can be shown that the REX quantifies the overall representation of a species with respect to its range, but should be complemented by species population trends for a final detailed assessment of the status of a species.

If we compare the REX values against species range it clearly demonstrates the inverse relationship of the two components – the wider the species range, the lower tend to be the REX value, though the variation at smaller range sizes tends to be higher (Fig. 3). This indicates the potential of REX, as it can differentiate between narrow-ranged species that are still well represented (high REX value) and species with a narrow range size, which are nevertheless underrepresented. Species of most concern are easily identified, namely species having a small range size and a small REX value.

Comparing the REX for different species groups demonstrates significant differences between groups (Fig. 4, $F_{5, 707}$ = 3.37, P < 0.01). Plants achieve the highest REX (3.51), followed by reptiles (2.41), invertebrates (2.37), fishes (1.59), amphibians (1.46) and finally mammals (1.44). This sequence is a consequence of the highly uneven number of studied species per group on the Annex II list, with plants being
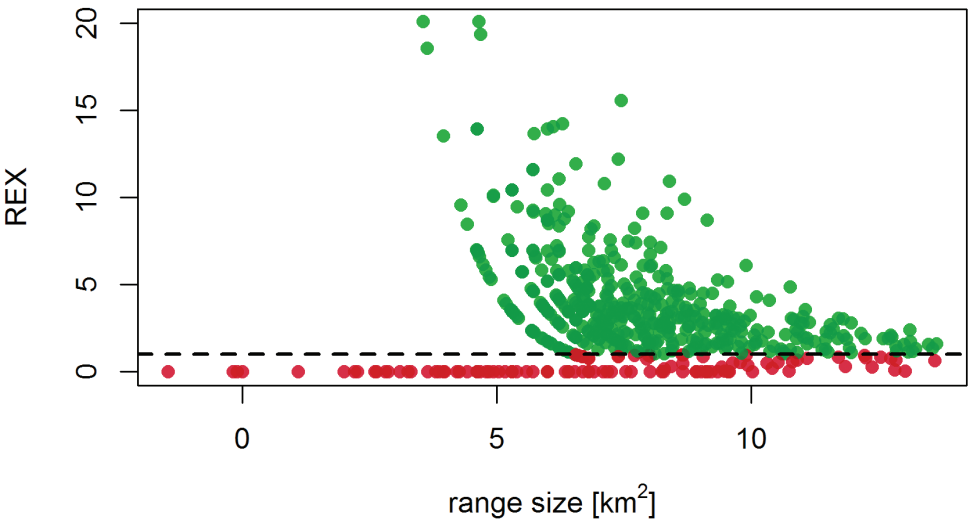
Figure 3. The relationship between species range sizes for 714 Annex II species and their associated REX value. Red dots indicate underrepresented species (REX < 1) and green dots overrepresented species (REX > 1). Note the log scale of the x-axis.
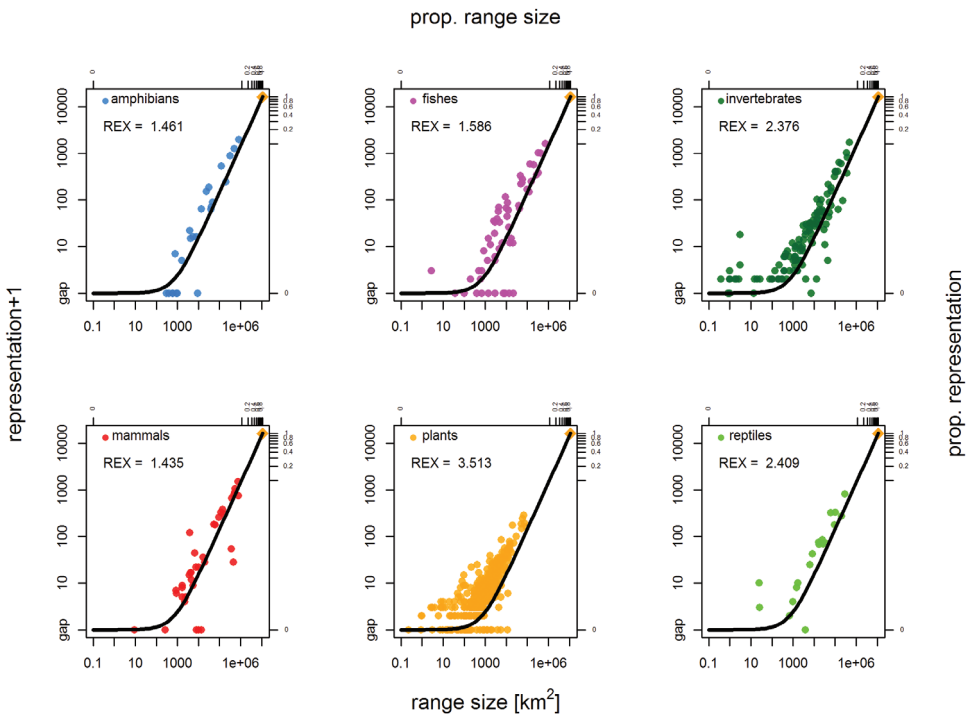

Figure 4. The relationship between species representation and range size for major taxonomic groups. The orange diamond indicates the maximum possible representation for a species distributed over the total area of the EU25 countries. REX is the median representation index for each species group.

the most prominent group, represented by 464 species, followed by invertebrates (114 species) and the other groups represented by a comparatively low number of species (19 reptiles, 24 amphibians, 34 mammals and 55 fishes). Therefore the comparison between species groups is most likely biased by the uneven distribution and the does not necessarily reflect species groups attributes.

The REX can also be used to compare the species representation status among countries (Fig. 5). Please note that here the basis to calculate the REX value for each species in a country is calculated using the area and the number of Natura 2000 sites of a specific country as reference. The REX values of the EU25 countries varies widely from about 0.3 (Lithuania) to over 25 (Cyprus). On average, all countries designated around 10-15% of their area to Natura 2000 sites (exception are Slovenia 31.4% and Spain 24.7%). This implies that countries with a lower number of Natura 2000 sites have on average designated sites with larger areas. Neglecting very small countries such as Malta and Cyprus, it can be seen that countries with a small number of larger sites (e.g. Portugal, Greece and Spain) achieve higher REX values than countries with many small sites (e.g. Czech Republic, Germany; Fig. 6).
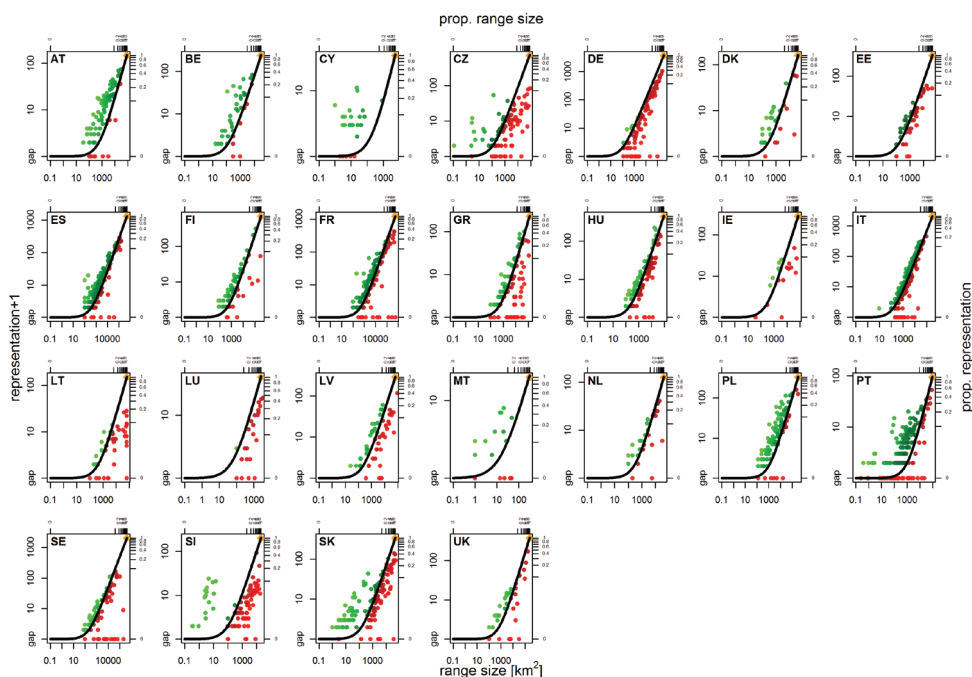

Figure 5. Representation as a function of species range sizes of Annex II species per EU25 country. The orange diamond marks the maximum possible representation of a species in a EU25 country occurring in the whole country. REX is the median represention index for each country. The coding of country names is as following: AT Austria, BE Belgium, BG Bulgaria, CY Cyprus, CZ Czech Republic, DE Germany, DK Denmark, EE Estonia, ES Spain, FI Finland, FR France, GR Greece, HU Hungary, IE Ireland, IT Italy, LT Lithuania, LU Luxemburg, LV Latvia, MT Malta, NL Netherlands, PL Poland, PT Portugal, RO Romania, SE Sweden, SI Slovenia, SK Slovakia, UK Great Britain.
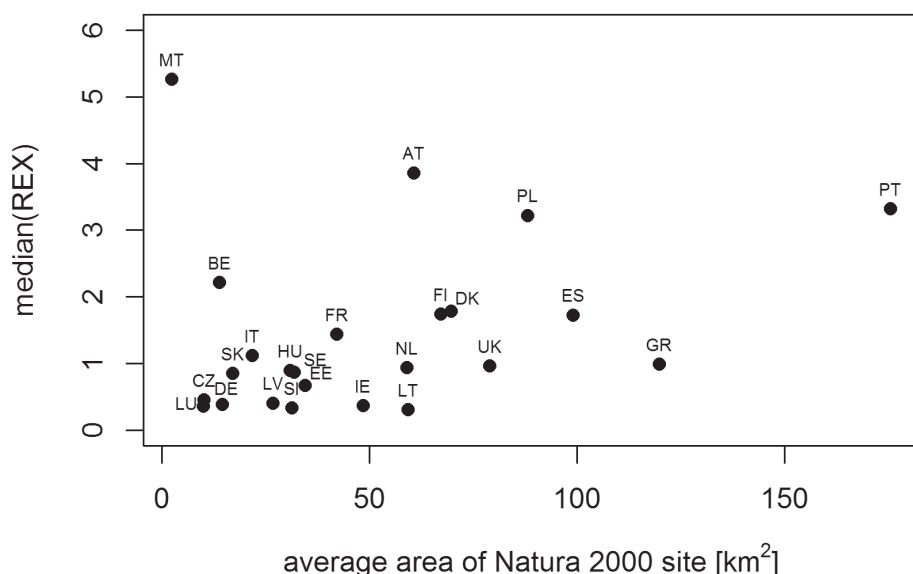
Figure 6. The relationship between average Natura 2000 and median REX value for each EU25 country.

Discussion

Our evaluation of the Natura 2000 reserve network found that the network adequately minimizes gap species by providing representation for many species of restricted ranges. It also demonstrates that the representation of Annex II species in the network is uneven, and it identifies species that currently have a low EU-wide representation. We argue that the representation of Annex II species and the derived representation index REX can be used to identify gaps in the Natura 2000 network and to guide future conservation effort.

Establishing a reserve network such as the Natura 2000 network will necessarily remain suboptimal to some degree. That is always the case in an opportunistic designation process limited by economical, cultural, political and scientific constraints, and one which builds on already existing national networks of protected areas (Knight and Cowling 2007). In many countries Natura 2000 has been largely based on existing protected areas (European Topic Centre on Biological Diversity 2005). Our results showed that this designation process leading to most species being represented as expected if sites were selected at random and an overrepresentation of wide ranging species (e.g. the Eurasian otter *Lutra lutra*, is listed in 3,185 sites). This indicates that there was relatively little coordination among countries in site selection. Notwithstanding, a certain level of coordination was achieved by "Biogeographical Seminars" (European Topic Centre on Biological Diversity 2005), which resulted in fewer gap species than expected if sites were selected at random. In these seminars, the designation of sites for each species was coordinated among countries sharing a biogeographic region (typically 2–6). We stress that we do not think that overrepresentation is a disadvantage for the species involved. However, we are convinced that it would be more effective to designate future Natura

2000 sites dependent on existing representations of species, considering the 2020 target of halting the loss of biodiversity and the limited resources available.

One might argue that the Natura 2000 network was established not only for species but also for habitats listed in Annex I of the Habitats Directive and therefore our analysis is not measuring the full benefit of the network. Nevertheless, as the REX index was below one for 115 of the 714 species (see Table S2 for species names), i.e. below the value expected by their range, this demonstrates that for these species the selection process for covering species was insufficient. So we would argue, even if the network is successful in covering habitats (which has not been demonstrated), it fails short in achieving a protection of all Annex II species (Moilanen and Arponen 2011).

Especially if national red lists are used in several countries independently there is a high chance that wide-spread species are well covered by the network and narrow to mid-ranged species are under-represented. A possible solution is provided by the idea of assigning different conservation responsibilities to countries, which reflects the contribution of a country or area to the survival of a species (Schmeller et al. 2008a; Schmeller et al. 2008b). We demonstrate the effect of using Annex list species as the main designation criteria, by comparing the achieved representation to the representation if species were randomly allocated to sites.

Assuming that countries selected their sites primarily for the rarer habitats and species to ensure they are covered by the network, the more common species will often occur in these sites and so inevitably emerge as highly represented. We conclude that to ensure the effectiveness of future designations, sites should not be designated primarily for wide-ranging Annex species that are already well represented elsewhere; rather the focus should be on underrepresented species.

In principle the same kind of analysis could be done for habitats, which are listed in the Habitats Directive and also reported by Article 17 of the Directive. We excluded these from our analysis as in our opinion the representation concept is less applicable to habitats. Habitat interpretations vary between countries, and sometimes between regions in the same country (e.g. Belgium and Spain; Evans 2010); in contrast populations of animal species, such as the Eurasian otter in Germany and the Czech Republic, still may belong to the same metapopulation. Therefore, we based our evaluation of the Natura 2000 solely on the Annex II species, neglecting the positive effects of the network on birds (Donald et al. 2007) and habitats. Our analysis is still an important evaluation of one of the central goals of the Habitats Directive, namely the protection of its Annex II species.

As the proposed REX index is calculated by a fraction of two values, there are in principle to ways to achieve a high REX value. Either having a high value in the numerator by protecting a species in a large number of sites or by having a small value in the denominator, which is easier achieved, if species have a small range size. Illustrated by an average REX value of 3.51, plants are highly overrepresented in the Natura 2000 network. A likely reason why plants are well covered is that many Annex II species have a fairly restricted range size, which allows for high REX values in this species group where Annex II includes many localised endemics, particularly in Macaronesia and the

Mediterranean. In contrast to this, it is much harder to achieve a high REX value for wide ranging species, such as many mammal species, which likely is the reason why the average REX value for mammals is the lowest among species groups. In addition, the REX is more sensitive (changes more quickly) if sites of narrow ranged species compared to wide ranged species are lost, which is a good characteristic for a representation index – hence it weights sites in accordance to their importance for a species.

On the scale of countries, the REX favours countries with fewer, but larger sites that protect more species at once. Countries with fewer and larger sites, such as Spain, have simply a smaller value in the denominator of the REX formula. Both ways to increase the REX value (having a large numerator or a low denominator) are desirable properties of the REX in terms of conservation, as it favours larger sites and obviously a representation in a large number of sites. Both size and number of sites are important factors contributing to the survival of species (Hanski and Gilpin 1997; Henle et al. 2004). The general notion that it is preferable to have fewer and larger sites (smaller denominator), if representation is achieved on a similar level, is in our view a too narrow proposal. A country with many smaller sites (larger numerator) may also achieve high representation despite societal constraints posed on the designation of sites (e.g. human population density, subsidiary governance structures).

Conclusions

Our evaluation of the Natura 2000 reserve network demonstrates that the site selection process succeeded in avoiding gap species but was inefficient as many species are underrepresented relative to expectation based on their range size. Despite this inefficiency the selection process led to species with smaller ranges being relatively better represented than wide-ranging species, as demonstrated by their higher REX index. Most importantly, our evaluation identified species that currently have a low EU-wide representation and should be targeted in further site designations. Here, in contrast to complex reserve site selection algorithms, our approach has the advantage to be rapid and simple. It thus can serve as a rapid assessment tool for elucidating effectiveness and deficiencies of the Natura 2000 network across the EU and within Member States and it is easily transferable to other developing reserve networks (Hartley et al. 2007).

Supporting information

Table S1, S2 are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Acknowledgements

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Appendix 1

Table S1: List of gap species in the Natura 2000 network (Natura 2000 database, June 2009, European Environmental Agency). (doi: 10.3897/natureconservation.3.3732. app1). File format: MS Exel Document (xls).

Explanation note: The table shows the 54 gap species ordered by species group. Please note: The comment column is based on expert opinion of the European Topic Centre, which has the latest version of the Natura2000 data base and also knowledge on confidential sites, which are deleted from the public version of the data base to protect rare species.

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Appendix 2

Table S2: List of 714 Annex II species (ordered by REX). (doi: 10.3897/natureconservation.3.3732.app2). File format: MS Exel Document (xls).

Explanation note: This table shows Eunis-Code, species name, species group and REX value of all Annex II species for all 714 that were included in the study, because complete distribution data from all EU25 member states were available.

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