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Original Research Article

The effectiveness of area protection to capture coastal bird richness and occurrence in the Swedish archipelago

Maria Nord [a], Åsa Ranlund [a, b], Lena Gustafsson [a], Victor Johansson [a, c], Tomas Pärt [a], Pär Forslund [a, *]

[a] Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden
[b] Department of Forest Resource Management, Swedish University of Agricultural Sciences, Umeå, Sweden
[c] Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91, Stockholm, Sweden

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A B S T R A C T

Protected areas are a key component in biodiversity conservation strategies, but evaluations of how effective they are in capturing species diversity is lacking for many ecosystems. We compared different protection types (animal sanctuaries, nature reserves and unprotected areas) using data on species richness and occurrence of coastal breeding bird species in a large archipelago in the Baltic Sea. Data were from extensive inventories based on a grid with 1×1 km resolution covering 4646 km^2 on the East coast of Sweden. We focused on specialist species breeding exclusively in coastal habitats since these species are of specific conservation concern, but considered generalists, which also breeds in inland wetlands, as well. Animal sanctuaries had significantly higher species richness of specialist species than unprotected areas and nature reserves. Nature reserves had even lower richness of specialist species than unprotected areas. Further, a rarity-weighted diversity index showed that animal sanctuaries were better in capturing hotspots of bird diversity compared to nature reserves and unprotected areas. Hotspots, both protected and unprotected, were scattered throughout the entire archipelago. The rarity-weighted richness is therefore useful to identify gaps in the protected area network. Overall, we conclude that the establishment of animal sanctuaries has been a successful conservation measure for protecting specialist species in several aspects. Ongoing human exploitation of the Baltic archipelagos prompt further consideration of protecting still unprotected but species rich shorelines for the benefit of many coastal breeding birds.

1. Introduction

Protected areas are often important to reduce population declines and extinction risks of species (Pimm et al., 2014), with the number of protected areas now exceeding 150 000 and approaching 15% of the global land area (Lewis et al., 2017; Watson et al., 2014). There are, however, different types of area protection, which might vary in their effectiveness of protecting populations. For birds, for example, there is a long tradition of conservation measures including areas designated specifically for their protection. Many studies compare bird species richness and abundance or occurrence among areas with and without protection (Barnes et al., 2015; Duckworth and Altwegg, 2018; Greve et al., 2011; Jackson et al., 2009; Virkkala et al., 1994), and some compare also different types of area protection (Abellán et al., 2011; Rayner et al., 2014). These empirical studies show

* Corresponding author.Department of Ecology, Box 7044, 750 07, Uppsala, Sweden.
E-mail address: par.forslund@slu.se (P. Forslund).

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that the effectiveness of area protection for promoting species richness and abundance of birds varies. The reasons for this variation remain unclear, but may depend on type of area protection. The question is therefore whether birds require area protection designed especially for them, or whether they also benefit from more generally motivated area protection.

There are several ways to assess the ecological performance of protected areas (Gaston et al., 2008). Often target species are used for assessment, such as species associated with specific habitats (specialist species). Locally, two straightforward ways of evaluation are to compare species richness (e.g. Greve et al., 2011), or target species abundance (e.g. Godet et al., 2007) in areas with or without protection. At a larger scale, assessment can include the ability of the protected area network to preserve a region's species pool (e.g. Evans et al., 2006). In addition, the precision of area protection can be tested by protected area coincidence with species rich areas, especially of rare species (a.k.a. 'hotspots') (Myers et al., 2000; Wu et al., 2013). This kind of evaluation also enables the identification of new priority areas for conservation (Rodrigues et al., 2004). Taken together, different forms of assessment can present a comprehensive analysis of protected area performance and, in addition, facilitate comparisons between modes of protection.

The effectiveness of protected areas may differ between species since type of protection may affect groups of species differently. In Sweden, two common types of area protection, regulated in the Swedish Environmental Code, are animal sanctuaries and nature reserves (SFS, 1998:808). One specific aim of animal sanctuaries in the Baltic Sea is to protect birds or seals, especially by prohibiting entrance during the time of reproduction. Nature reserves are created with broader conservation aims (i.e. to protect biodiversity, protect or manage valuable environments in general or for certain species, or to meet human recreational needs) (SFS, 1998:808). Therefore, animal sanctuaries often offer a stronger protection for birds because of prohibitions to visit the land and sometimes even surrounding waters during spring and summer.

Coastal habitats often host a rich bird fauna. In particular, archipelagos offer diverse bird habitats with mosaics of various vegetation types on islands and their shorelines, mixed with open waters. At the same time, coastal areas are often subject to extensive human exploitation, which can negatively affect birds. On the eastern coast of Sweden there are wide-ranging archipelagos in the Baltic Sea, which is a large inland sea with brackish water (Fig. 1). Water quality and shoreline habitat in the Baltic Sea have been heavily affected by various types of human exploitation, such as nutrient leaching from agriculture, settlements and boat traffic (Nord and Forslund, 2015; Ottvall et al., 2009; Sundblad and Bergström, 2014). Over the same time, covering decades, protected areas have been formed in the Swedish archipelago as animal sanctuaries or nature reserves. Although studies have been performed on breeding bird habitats and ecological gradients in this area (Nord and Forslund, 2015; Rönkä et al., 2008; von Numers, 1995), and on single or few bird species (Heinänen et al., 2012, 2008; Heinänen and von Numers, 2009), no study has so far targeted the effectiveness of protected areas in capturing coastal bird diversity.

Our aim was to assess the effectiveness of animal sanctuaries and nature reserves in terms of coastal breeding bird richness and occurrences of individual species both locally and at a regional level. For our analyses we used extensive and complete coastal bird inventories in archipelagos embracing >50,000 islands (Statistics Sweden, 2009) and including protected as well as unprotected areas. The inventories were done by regional authorities in eastern Sweden using a spatial resolution of grids with 1×1 km squares. Due to the different reasons for protection (see above), we predicted bird species richness and occurrence to be higher in animal sanctuaries than in unprotected areas, with a less distinct contrast between nature reserves and unprotected areas. In our analyses we emphasised breeding species confined to the coastal landscape (hereafter specialists), although a few also occur in restricted areas in the inland of northern Sweden. We also investigated the patterns for species that, additionally, can breed in inland wetlands, e.g. lakes and ponds (hereafter generalists). These two species categories were compared among animal sanctuaries, nature reserves, and unprotected areas regarding local species richness of the 1×1 km squares. Further, we analysed local species occurrence of breeding pairs with regard to the types of protected areas and unprotected areas. Finally, we used regional-level measures to investigate the ability of the different areas to contain the regional pool of species, and to identify conservation hotspots for specialist species to test whether there was a spatial association between hotspots and type of protection.

2. Material and methods

2.1. Study area

The study area is situated in the Baltic Sea on the east coast of Sweden, ranging from 58°36′N, 16°48′E in the south to 60°39′N, 17°33′E in the north (Fig. 1). The islands that make up the study area vary in size from small islands almost entirely consisting of bare rock, to large islands of the size of several km^2, covered with dense forest (Ås et al., 1997). In addition, the study area consists of the coastline of the adjacent mainland, where the shoreline habitat varies from high vegetation to bare rock. The area is under isostatic uplift at a rate of approximately 5 mm/year (Ericson and Wallentinus, 1977). This has resulted in a general zonation of the archipelago into an inner-, middle- and outer part, with generally larger islands in the inner parts and smaller islands in the outer parts. The water is brackish and there are no tides.

2.2. Bird survey

Coastal breeding bird species, all with some degree of dependency on shoreline habitat for breeding, were inventoried between the years 2000 and 2004 (Table S1). Bird counts were restricted to land within 100 m of the shoreline. In each of the

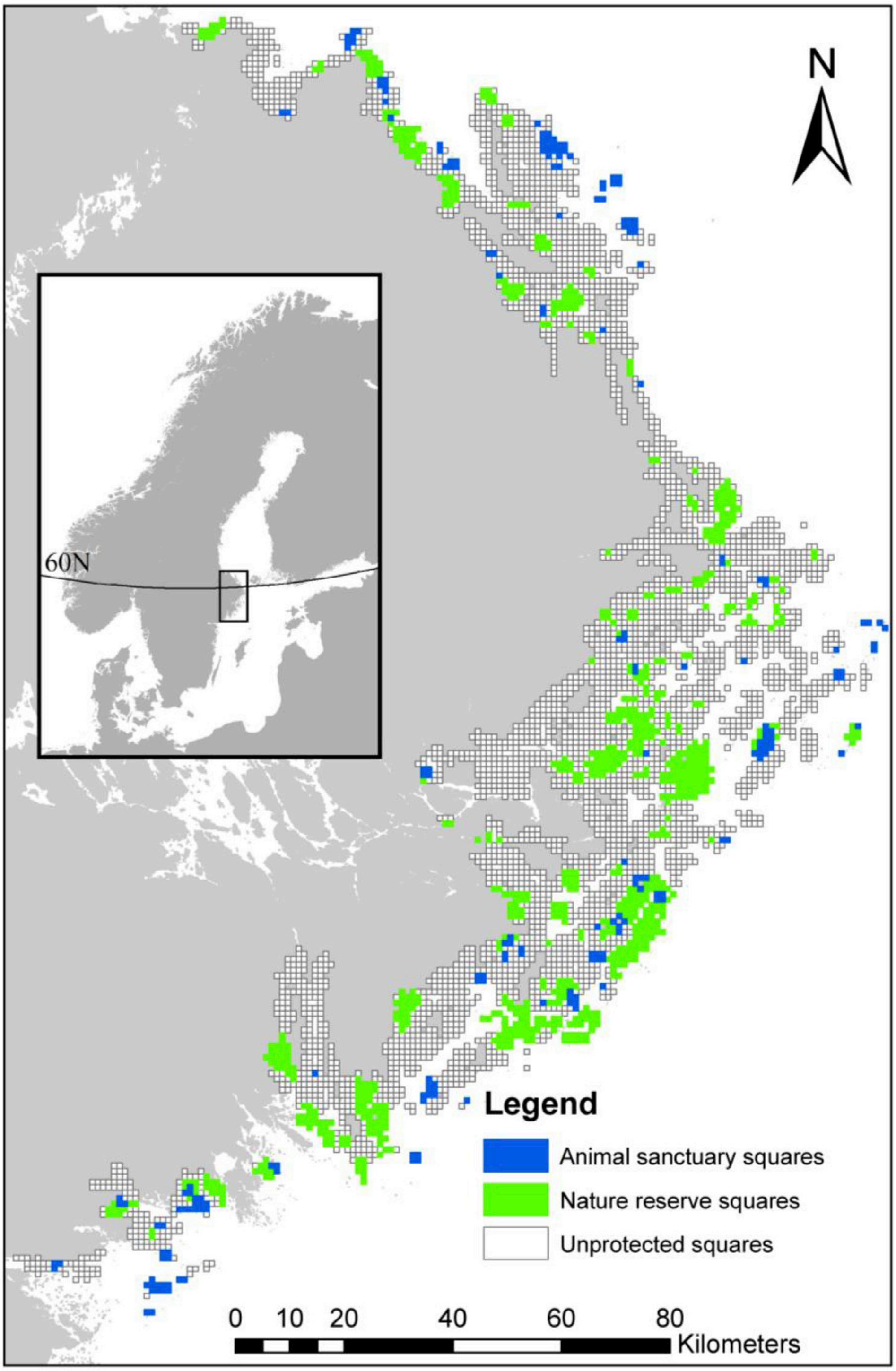

Fig. 1. Map of Fennoscandia and the study area with all 1×1 km squares in which coastal breeding birds were inventoried (4646 squares in total). Blue squares were classified as animal sanctuaries, or both nature reserves, and animal sanctuaries, while green squares were classified only as nature reserves. The classifications were based on protected areas established prior to 2003. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4646 1 km^2 squares (Fig. 1) abundance of breeding pairs was summarised for each species, with the exception of Rock Pipit where only presence was recorded. In order to ascertain that species with different breeding phenology would be observed, the bird surveys were conducted over three occasions, in April, May and June. Inventories were carried out by teams of two or three people on calm days without fog or rain. Birds were assumed to be breeding based on a combination of observations of parental behaviour, birds seen on nearby water (April and May) and nests found on land (June) (Olsson, 2000). All field workers were experienced bird watchers following the same detailed instructions. For further details concerning the inventory, see Nord and Forslund (2015). The bird species were classified as either coastal specialist species (n = 19), or coastal generalist species (n = 29) according to distribution maps in Svensson et al. (1999)(1999).

2.3. Protected areas

Squares were classified into three categories of types of shorelines with regard to protection: 1) unprotected squares (<5 m protected area shoreline, n = 3554), 2) nature reserve squares (≥5 m shoreline belonging to a nature reserve, n = 877), and 3) animal sanctuary squares (≥5 m shoreline belonging to an animal sanctuary, n = 215) (Fig. 1). These categories are hereafter called protection types. Squares with shorelines belonging to both nature reserves and animal sanctuaries were classified as animal sanctuaries (n = 84), since the latter represent a stronger type of protection for birds (Table S2).

2.4. Environmental variables

Three environmental variables were included in the study to account for factors already known to be of importance to coastal breeding birds (Nord and Forslund, 2015), thereby better separating the effect of protection type. All variables describe large-scale characteristics: land area per square, distance to open sea (shortest distance from each square's midpoint to a buffer line 150 m outside the islands furthest out to sea), and total shoreline length per square. For calculations of the shoreline length within nature reserves and animal sanctuaries, respectively, we used GIS-layers displaying protected areas established up until and including the year 2003. Information was extracted using ArcMap 9.2 software (ArcGIS, ESRI, Redland, CA, USA). For further details about GIS information, see Nord and Forslund (2015).

2.5. Statistical analyses

2.5.1. Local species richness

We modelled the local richness of specialist and generalist coastal bird species in relation to type of area protection (animal sanctuaries, nature reserve and unprotected). We used generalized linear mixed models with Poisson distribution and incorporated spatial autocorrelation using Integrated Nested Laplace Approximations (INLA, www.r-inla.org) in R. As a response variable we used the number of species per square for specialist and generalist species, respectively, and for both analyses we used three continuous explanatory variables measured at the level of the square: the length of shoreline, the distance to the sea, and the amount of land area. In addition, we used two dummy variables denoting the presence of protected areas of animal sanctuaries and nature reserves to categorize the three area protection types. The continuous explanatory variables were standardized to mean 0 and standard deviation 1.

To account for spatial autocorrelation we used a mesh with 5713 vertices (Fig. S1). We then used the Matérn covariance function to specify spatial correlation in the stochastic partial differential equation (SPDE) model (Lindgren et al., 2011), using the inla.spde2.pcmatern-function, with a prior range of 30 km with a probability of 0.001 for it to be lower, and a prior of sigma specified as 0.5 with a probability of 0.5 for it to be higher.

2.5.2. Local species occurrence

To investigate if individual species were more likely to occur in animal sanctuaries and nature reserves as compared to unprotected areas we first modelled the occurrence of breeding pairs as a function of protection type (animal sanctuary and nature reserve, with unprotected area as reference) for each species separately. We used a bernoulli distribution and a logit-link function, and the same explanatory variables as in the models for local species richness. We also modelled spatial autocorrelation in the same way as described above, with the same mesh and settings. Secondly, we modelled the size of the parameter estimates obtained for each species based on the binary explanatory variable of generalist or specialist to test whether any group was more tightly related to a protection type than was the other. Greater Scaup, Red-necked Grebe, Little Ringed Plover, Black-throated Diver, Common Murre, and Pintail all lacked breeding pairs in animal sanctuary squares or nature reserves and were therefore excluded from the analyses.

2.5.3. Regional-level measures

We used sample-based rarefaction curves (calculated with 1000 replications) to compare the total number of specialist and generalist species, respectively, between the three protection categories, as a measure of how well the different protection types might preserve the region's species pool. We used the estimateD-function (Hsieh et al., 2014) to compare the effectiveness of the different protection types in capturing specialist bird species richness also in small areas.

Hotspots for specialist species and their overlap with protected areas were investigated by a scoring method, rarity-weighted richness (RWR, Guerin and Lowe, 2015; Williams et al., 1996). Each specialist species was assigned a weight based on the inverse of the number of squares the species occupied (i.e. giving higher weights to rare species). For every square the weights of the occurring species were then summed, following Williams et al. (1996):

$$RWR = \sum_{\substack{i:c_i \neq 0,\\ 1 \le i \le n}} (1/c_i)$$

where c_i is the number of squares occupied by species i, and n is the total number of species. We were interested in mapping species hotspots, which can be defined by applying cut-off values where squares with RWR-scores above the cut-off are defined as hotspots. Such cut-offs are arbitrary, and we analysed two levels aiming for the 20% and 5%, respectively, of squares with the highest RWR (Fig. S2). The association between hotspot squares and protection type (i.e. animal sanctuary, nature reserve or unprotected) was analysed by the presence/absence of hotspots as a function of the three protection categories using a GLM with a binomial distribution ($n = 4646$). Simple conservation value indices, like the rarity-weighted richness, have in certain respects been evaluated as being at least as good as more advanced methods (Albuquerque and Beier, 2015; Csuti et al., 1997).

Analyses were performed in R version 3.4.4 (R Development Core Team, 2018) using the INLA package for the GLMMs (Rue and Martino, 2009) and the iNEXT package for the rarefaction analyses (Hsieh et al., 2014).

3. Results

3.1. Bird data and environmental variables

In the 4646 surveyed 1×1 km squares a total of 48 species were recorded, comprising 29 generalists and 19 specialists. All species were found in squares without protection, while 44 species were recorded in squares with nature reserves and 44 in squares with animal sanctuaries (Fig. 2, Table S1). Four percent of the squares had no species, while species richness in occupied squares varied greatly and ranged from 1 to 25 (Table S3). In total 209 416 breeding pairs were recorded (27 934 occurrences); 144 452 in unprotected squares (20 873 occurrences), 36 126 in nature reserves (5275 occurrences), and 28 838 in animal sanctuaries (1786 occurrences). Summaries of breeding pair occurrences and abundances with regard to species, protection type and species group are shown in Tables S1 and S3.

Animal sanctuary squares had on average a smaller land area than nature reserve squares and unprotected squares, and the animal sanctuary squares were on average also found at a comparatively short distance from the open sea (Table S4). The variation of these environmental variables was, however, large (Table S4).

3.2. Local species richness

The average number of species per square, for both specialist and generalist species, was higher in animal sanctuary squares than in unprotected squares while accounting for other influential environmental variables of square characteristics (1.29 and 1.19 times higher, respectively, for specialist and generalist species; Table 1). For specialist species the average richness in nature reserve squares was, in contrast, lower than in unprotected squares (0.95 times lower for specialist species; Table 1).

3.3. Local species occurrence

Most species were more likely to be found in animal sanctuary squares compared to unprotected squares (Fig. 3a) although the 95% confidence intervals for the parameter estimates were overlapping zero for several species. However, for 12 species (including 8 out of 14 analysed specialists) the parameter estimate for animal sanctuary presence was positive with confidence intervals that did not overlap zero (Fig. 3). In contrast, no species had significantly fewer breeding pairs in animal sanctuaries (Fig. 3a). Specialist species as a group had significantly higher mean parameter estimates for the comparison between breeding pair occurrence in animal sanctuary squares and unprotected squares (i.e. they were more positively related to animal sanctuaries) than generalists (mean estimate = 0.41, CI 0.04–0.79). For the comparison between breeding-pair occurrences in nature reserve squares and unprotected squares, one specialist species (Velvet Scooter) occurred significantly more in nature reserve squares while seven species (three specialists: Common Eider, Arctic Jaeger, and Eurasian Oystercatcher; four generalists: Common Pochard, Common Gull, Gadwall, and Eurasian Coot) occurred significantly less there (Fig. 3b). There was no significant difference between estimates of specialist and generalist species in explaining response to nature reserve squares (mean estimate = 0.08, CI -0.07–0.22). For five species the models did not converge: Eurasian Widgeon, Eurasian Curlew, Garganey, Razorbill and Rock Pipit.

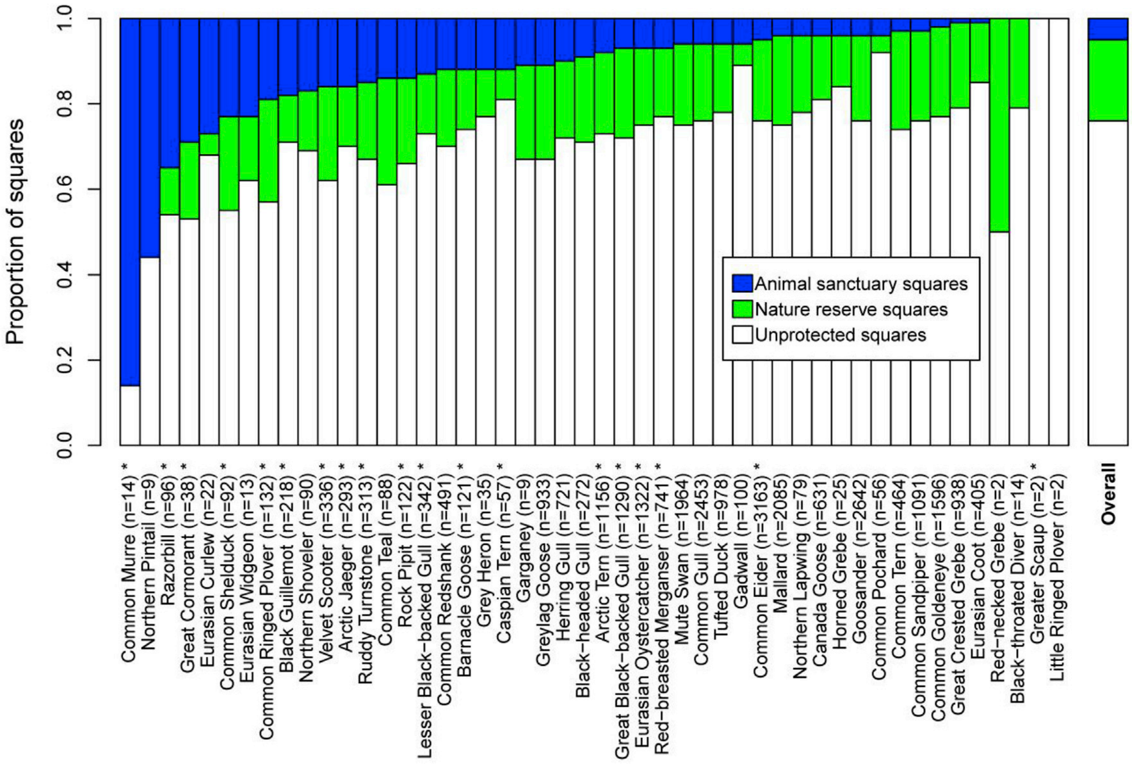

Fig. 2. The proportion of squares classified as either animal sanctuaries, nature reserves or unprotected areas where each species occurred. Specialist species are marked in bold. n is the total number of squares in which the species occurred.

Table 1
Number of breeding bird specialist and generalist species per square in relation to protection type and environmental variables. Unprotected squares form the baseline. For each estimate the mean and confidence interval (CI) is presented. Statistical inference is drawn from whether confidence intervals overlap zero or not.

	Specialists		Generalists	
	Mean	CI	Mean	CI
Intercept	0.23	0.14–0.30	0.62	0.58–0.65
Animal sanctuary	0.25	0.15–0.35	0.18	0.08–0.27
Nature reserve	−0.05	(-0.09) – (−0.01)	−0.01	(-0.04) – 0.02
Distance to sea	−0.28	(-0.39) – (−0.15)	0.09	0.04–0.15
Land area	−0.52	(-0.56) – (−0.48)	−0.10	(-0.12) – (−0.08)
Length of shoreline	0.26	0.24–0.29	0.34	0.32–0.36

3.4. Regional measures

3.4.1. Rarefaction

The rarefaction analysis showed that the total number of species in animal sanctuaries, nature reserves and unprotected areas accumulated up to similar numbers of specialist and generalist species, respectively (Fig. 4). However, the number of species accumulated much faster in animal sanctuaries than in nature reserves and unprotected areas (Fig. 4), especially for specialists with an estimated accumulated richness of 17.1 species (95% CI: 16.6–17.5) already at 30 sampled animal sanctuary squares where the same area gave 11.8 (95% CI: 11.4–12.2) and 11.9 (95% CI: 11.7–12.1) species for nature reserve and unprotected squares, respectively.

3.4.2. Hotspots

The classification of squares as hotspots was explained by the occurrence of animal sanctuaries, both when hotspots were defined as the 5% and 20% of squares with highest rarity-weighted richness (Table 2). Whether squares were situated in nature reserves or not had, on the other hand, no significant effect on hotspot classification (Table 2). Half of the animal sanctuary squares had RWR-scores that were among the top 20% RWR-scores, whereas only 14% of nature reserve squares and

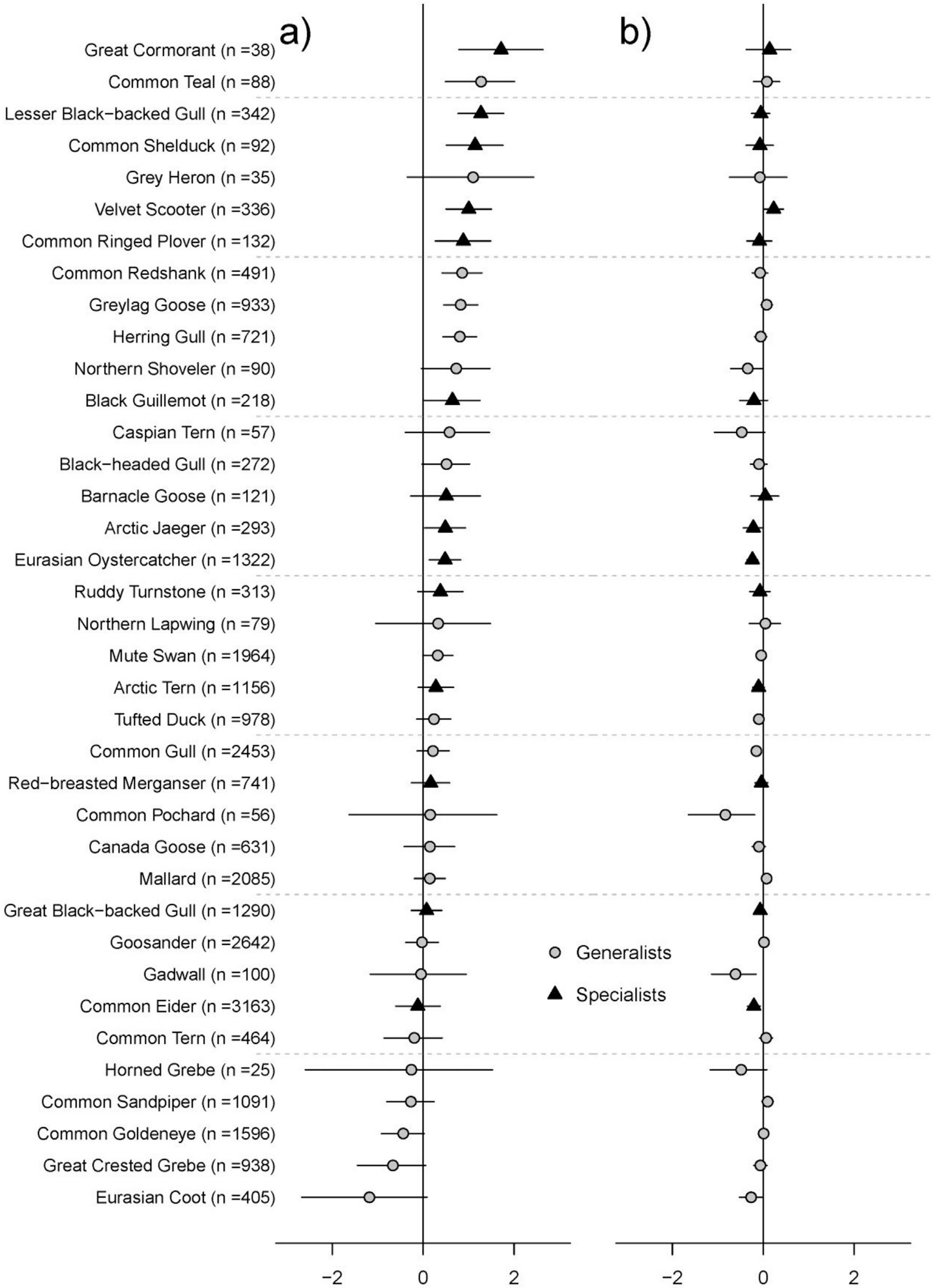

Fig. 3. Parameter estimates, with 95% confidence intervals of occurrences in a) animal sanctuary squares compared to unprotected squares, and b) nature reserves compared to unprotected areas. Species with positive parameter estimates have more occurrences of breeding pairs in animal sanctuary or nature reserve squares, respectively, compared to unprotected squares, while negative parameter estimates indicate more occurrences of breeding pairs in unprotected squares when the confidence intervals do not overlap with zero. Some species were not included for various reasons (six species lacked occurrences in either animal sanctuary squares or nature reserve squares, and for five species the models did not converge).

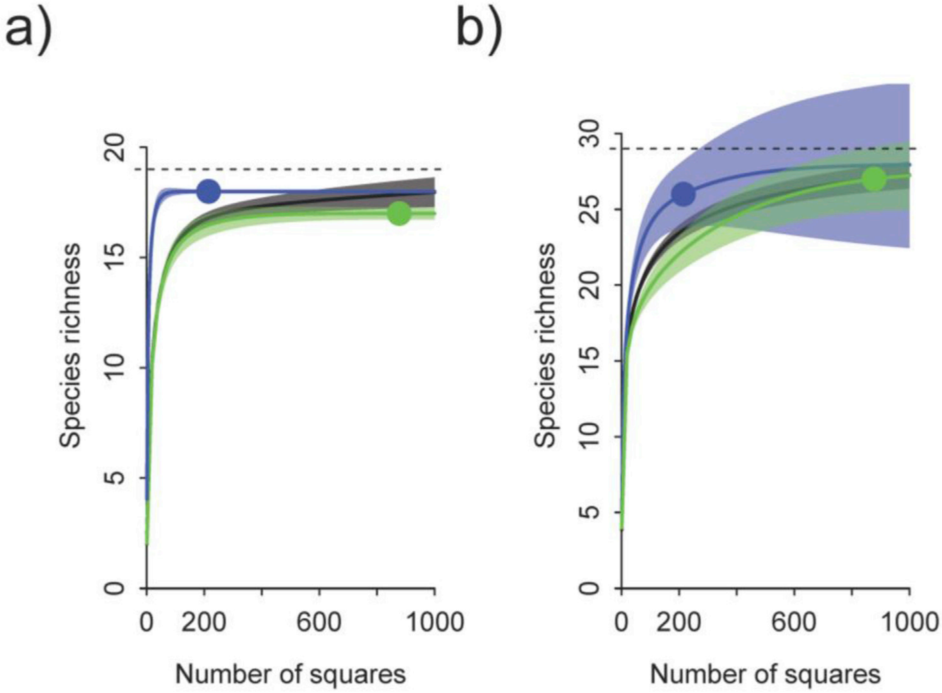

Fig. 4. Sample-based rarefaction curves for a) specialist species and b) generalist species. Solid lines are the rarefaction curves and shaded areas are 95% confidence intervals. Blue represents animal sanctuary squares, green represents nature reserve squares, and black represents unprotected squares. The dashed top lines indicate the total number of species for each group; 19 specialist species and 29 generalist species. The circles represent the surveyed number of squares of a protection type, so that the rarefaction line to the left is interpolated and to the right it is extrapolated (the circle for unprotected squares is beyond view since n = 3554). Note the different scales on the y-axes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Comparison of how species hotspots, based on rarity weighted richness (RWR), relate to the distribution of squares with different protection categories. For two hotspot levels (the 5% and 20%, respectively, of squares with highest RWR) we analysed whether the presence/absence of hotspots was explained by protection type (using a binomial model). The number of squares are amount of squares with the 5- and 20% highest RWR, and therefore the sample sizes for these analyses.

Cut-off	Animal sanctuary		Nature reserve		Number of squares
	Mean	CI	Mean	CI	
5%	2.17	1.82–2.52	0.01	−0.38–0.38	232
20%	1.80	1.51–2.08	0.04	−0.16–0.23	932

unprotected squares, respectively, were among the top 20% RWR-scores. A minority of the hotspot squares were protected: 40% out of 232 (5%-level) and 31% out of 932 (20%-level).

Since the RWR-score depends on species richness and on the species-abundance distribution within the area studied (Fig. S2), a high RWR-score can be the result of relatively few rare species (since rare species are assigned large weights) or many common species (see the equation for RWR estimation in the Methods section). The mean weight ($\overline{1/c_i}$) for species occurrences in animal sanctuary squares was 3.9×10^{-3}, whereas it was 1.6×10^{-3} and 1.8×10^{-3}, respectively, for nature reserve and unprotected squares. Since rare species have higher weights ($1/c_i$), the mean weights indicate that there was a higher density of rare species in animal sanctuary squares than in nature reserve or unprotected squares.

4. Discussion

The results from this study suggest that the formation of animal sanctuaries along the Swedish coast has been successful in terms of protecting a high richness and probability of occurrence of breeding coastal specialist bird species. Compared to unprotected areas, the animal sanctuaries hosted a 1.29 and 1.19 times higher richness, respectively, of coastal specialist and generalist species, and many coastal specialists had a distinctly higher probability of breeding in animal sanctuaries than elsewhere. Furthermore, the animal sanctuaries appeared to be especially associated to the rarest specialist species. Thus, our results confirm the prediction that bird species richness, as well as the occurrence of many species, is higher in animal sanctuaries than in unprotected areas. Nature reserves, on the other hand, had lower species richness of specialists compared to unprotected areas, and several species occurred less there. Our results confirm other studies showing that bird diversity can indeed be higher in protected areas than in unprotected areas (see references in Introduction). More importantly, our study also points at the importance of diversifying between different types of protected areas (Abellán et al., 2011; Rayner et al., 2014), as we found that animal sanctuaries had higher species richness than both nature reserves and unprotected areas.

4.1. Area protection and local species richness and occurrence

There may be several explanations for the effectiveness of animal sanctuaries in capturing species richness and occurrence of coastal breeding bird species. Gaston et al. (2008) argue that one reason that protected areas seem effective could be that protection is established in places of high species richness or occurrence of certain species. In our study, such examples may include Common Murre and Razorbill which have breeding populations highly aggregated to certain islands, many of which have since long been protected with the specific aim to secure the long-term survival of these species. The fact that especially specialist species still are abundant in animal sanctuaries, even though some areas were formed some 30 years prior to the bird inventory, indicate that the sanctuary network has a long-term function. A second reason could be that protected areas, although they originally might have had similar species richness compared to unprotected areas, have faced lower levels of disturbance so that more species have been able to settle there (Gaston et al., 2008). The County Administrative Boards have imposed regulations that prohibit humans to enter some animal sanctuaries during the breeding season, especially in the outer part of the archipelago. This may have contributed to increased species richness and occurrence of species that prefer to nest in undisturbed areas, perhaps due to a redistribution of birds from other areas into undisturbed areas. However, testing whether reduced anthropogenic disturbance affects species requires time series data, which were not available in the present study. Hence, it is still an open question whether the higher richness of animal sanctuaries is explained by high initial species richness or increased richness due to the protection. It is also possible that there are different explanations for different animal sanctuaries. Irrespective of which the explanation is, our results show that the animal sanctuaries protect a high species richness of coastal breeding birds and thus in an important conservation measure.

Local bird species richness was lower in nature reserve squares than in unprotected squares for specialist species. One possible reason for that is the often broad aims of nature reserves that are unrelated to birds (e.g. protecting vascular plants, maintaining habitats belonging to historical agricultural land-use, or for recreational purposes) (Statistics Sweden, 2014), several of which may be associated with habitats (e.g. high vegetation) that repel coastal breeding birds. Further, a possible side effect of recreation in nature reserves is an increase in the rate of human visits (hiking, camping etc.) and the associated disturbance may be negative for breeding success of some bird species, like waders. Our results agree with Rayner et al. (2014)(2014) who also found that reserves not specifically designated for bird conservation had lower bird species richness and occurrence than unprotected areas.

4.2. Area protection and regional species richness

The hotspot analysis showed that animal sanctuaries hosted a much larger proportion of specialists, weighted by rarity, than expected by chance. Our analysis also shows a mosaic distribution of squares with high rarity-weighted richness, without strong regional aggregations (Fig. 5). We therefore find no support for regional prioritizations, but instead a need for more fine-scale conservation planning based on for example present occurrences of some species or environmental characteristics like proximity to open sea.

The rarefaction analysis showed that animal sanctuaries captured occurrences of almost all of the specialist coastal bird species in the region (17 out of 19 species), and that a rather small area of animal sanctuaries would be needed to accumulate most of the species compared to nature reserves or unprotected areas. When considering the hotspot and the rarefaction analyses together, animal sanctuaries seem efficient in capturing coastal bird species diversity. Nature reserves and unprotected areas accumulated the species at a slower rate and did not reach the same number of species, although it should be noted that a few of generalist species (Fig. 2) were present only in these categories and not in sanctuaries. Regarding generalist species, there was no clear difference between protection categories in the accumulation of species, and the rarefaction analysis indicated that all categories were needed to assemble all generalist species.

4.3. Implications for conservation planning

The main conclusion from this study is that the establishment of animal sanctuaries has been a successful conservation measure for protecting specialist species. However, the hotspot analysis revealed that there are many unprotected areas that host specialist species, of which many are uncommon. Since our study is based on inventories performed at one point in time we do not know anything about the population dynamics of the specialist species, e.g., if there are any negative population trends. Hence, the hotspot areas identified by our hotspot analysis indeed would be worth protecting, if still unprotected, to ensure long-term survival of specialist species.

Overall, nature reserves as well as unprotected areas should overall be recognized as important for maintaining coastal bird populations (e.g., unprotected areas covered a 17 times larger area than animal sanctuaries and had almost 99 500 breeding pairs of specialist species, i.e. 67% of the total numbers). To further evaluate the importance of the vast but

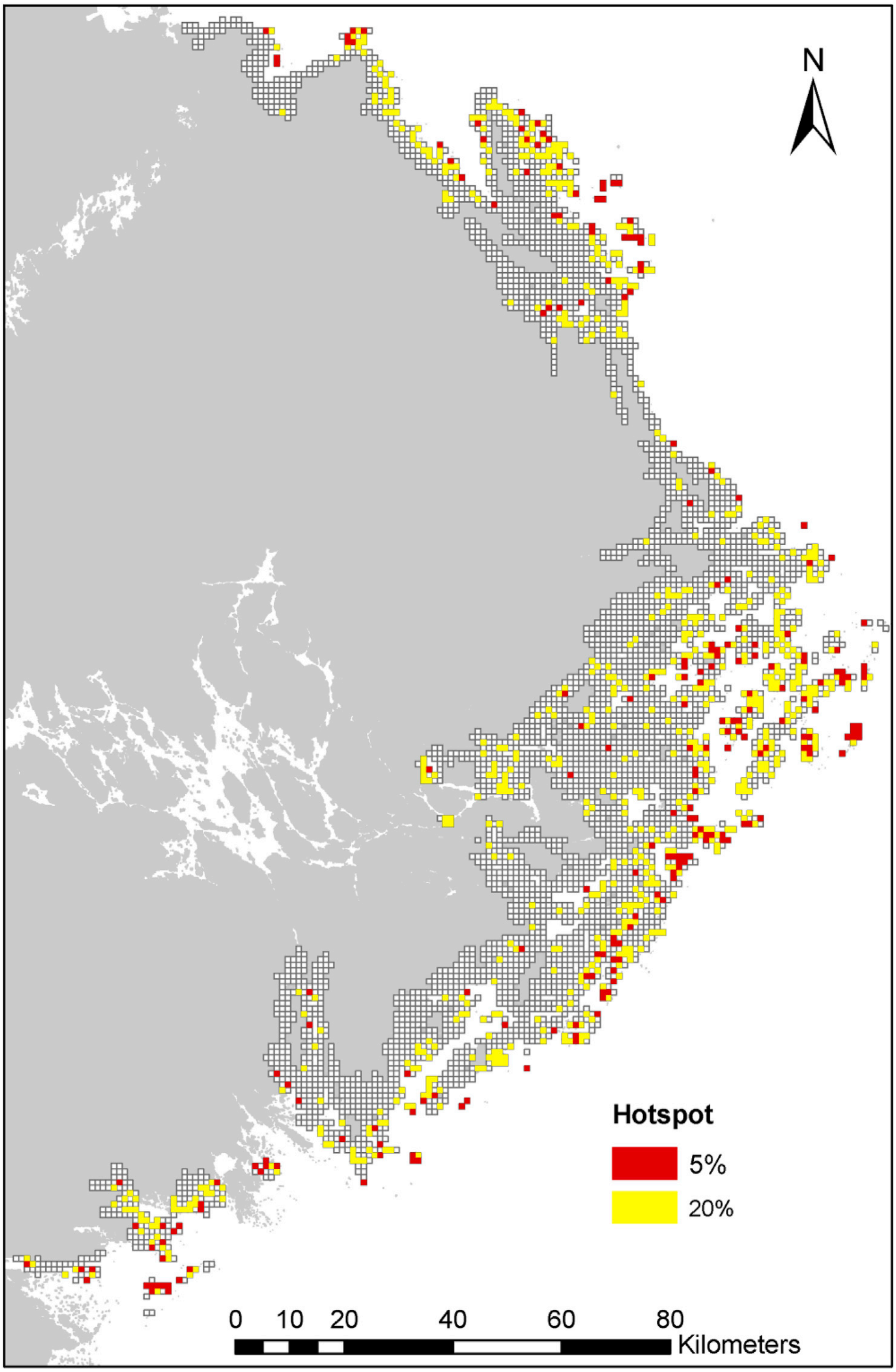

Fig. 5. Classification of squares based on the hotspot analysis. Hotspots are mapped for two levels: 5% (red squares) and 20% (yellow squares) of squares with the highest rarity-weighted richness. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

unprotected areas, the analysis should preferably be scaled up to embrace a larger geographical area, i.e., the entire of the Baltic Sea. By expanding the geographical scope, cross-national assessments could be made and used as a basis for large-scale conservation strategies. Such planning is motivated by the fact that human exploitation of shores is accelerating in the region (e.g. Nord and Forslund, 2015; Sundblad and Bergström, 2014) with settlements and associated disturbance that may affect many specialist birds in a negative way. Careful development planning will be essential, especially in the outer parts of the archipelago, since these are prime areas for coastal breeding specialists (Nord and Forslund, 2015).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00528.

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