Spatial Patterns of Coastal Breeding Birds in the Baltic Archipelago

Ecological Factors, Human Impact and Conservation

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Abstract

Coastal areas are crucial to numerous breeding bird species, but have undergone major changes because of anthropogenic development pressures such as altered land use and increased recreational activities. An understanding of what shapes species distribution patterns, and how human activities affect these patterns, is therefore necessary for marine management. The aim of this thesis is to investigate possible causes of spatial patterns of coastal breeding birds, and how human activities and environmental legislation affect these species. Forty eight coastal breeding bird species were surveyed in 4,646 squares of 1 × 1 km size, covering an archipelago in the Baltic Sea, on the east coast of Sweden. We classified all bird species as either specialist species, i.e. specialized coastal breeders, or as generalist species, i.e. species breeding also inland. Specialist species were found further out to sea, while generalist species were found closer to the mainland. The number of specialist and generalist species per square increased as total shoreline length increased, likely because of availability of suitable breeding habitat and feeding areas. Animal sanctuaries were significantly more effective in capturing specialist species and red-listed species than were unprotected areas, while nature reserves often were less effective compared to unprotected areas. Further, specialist species richness decreased as human shoreline exploitation such as buildings and jetties increased, while there was no significant effect on generalist species richness. Likewise, there was a higher probability of applications for exemptions from the general shore protection regulation to occur in squares with fewer specialist species. It is possible that habitats for specialist species are not appropriate for exploitation or that human disturbance make specialist species avoid exploited areas. The proportion of granted exemptions was very high (96%), and the areas they concerned were often close to previously exploited areas. Exploitation of shores is a continuous but slow process known as the cumulative effects problem or the 'tyranny of small decisions made singly', and this is difficult to tackle by environmental legislation. To conserve the breeding habitat along the shorelines in the archipelago, it is necessary to protect the shoreline against further exploitation, and appropriate management of unprotected shorelines is essential.

Keywords: biodiversity, archipelago, Baltic Sea, birds, avian richness, avian abundance, environmental gradients, protected areas, shoreline exploitation

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Dedication

To my family.

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Nord, M. & Forslund, P. (2015). Environmental gradients explain species richness and community composition of coastal breeding birds in the Baltic Sea. *PLoS ONE* 10(2): e0118455.

II Nord, M., Gustafsson, L., Johansson, V., Pärt, T. & Forslund, P. The effectiveness of protected areas for capturing coastal bird diversity in the Swedish archipelago (manuscript).

III Nord, M., Pärt, T., Glimskär, A., Kindström, M. & Forslund, P. Effects of shore exploitation on coastal bird diversity in the Stockholm archipelago (manuscript).

IV Forslund, P. & Nord, M. Application of the Swedish shore protection regulation in the Baltic Sea archipelago in relation to the diversity of coastal breeding birds (manuscript).

Papers I is reproduced with the permission of the publisher.

The contribution of Maria Nord to the papers included in this thesis was as follows:

I Main author and analysis. Developed research questions and design and wrote the paper together with PF.

II Main author and co-responsible for analysis (together with VJ). Developed research questions and design and wrote the paper together with LG, PF and TP.

III Main author and analysis (with contribution of MK). Developed research questions and design and wrote the paper together with PF, TP and AG.

IV Second author and co-responsible for analysis. Developed research questions and design, extracted data and participated in writing the paper together with PF.

1 Introduction

1.1 Background

Habitat loss is an important cause of species declines and extinctions (Brook *et al.*, 2003; Fahrig, 2003), especially in coastal ecosystems (Airoldi & Beck, 2007). At the same time, the extent of most metropolitan areas is expanding into adjacent rural landscapes (UN, 1997). This is also true in the Baltic archipelago on the east coast of Sweden, which is subjected to increasing shoreline exploitation (Sundblad & Bergström, 2014; Kindström & Aneer, 2007) as well as increasing recreational activities (Swedish Transport Agency, 2010). This is a cause for concern, as the archipelago is the home of a great number of species (Jerling & Nordin, 2007), many of which are red-listed (Sandström *et al.*, 2015). Hence, the biodiversity in the archipelago may be at risk due to habitat loss caused by exploitation.

Coastal breeding birds may be a particularly vulnerable group given that approximately 24% of all waterbird species were categorized as Globally Threatened in the IUCN Red List 2012 (Wetlands International, 2012; Croxall *et al.*, 2012; Butchart *et al.*, 2010; Ottvall *et al.*, 2009). The coastline and archipelago of eastern Sweden is an area of great importance for breeding coastal birds, both nationally and internationally. Indeed, several surveys and local inventories have suggested that the bird fauna along the Swedish east coast has gone through large changes recently (Pettersson, 2005). Thus, knowledge about the spatial patterns of bird species diversity and the ecological and human-mitigated factors that affect it are needed for an efficient management of bird populations in the heavily exploited coastal zone.

Figure 1. Two typical islands in the middle of the Stockholm archipelago. The island in the top figure is characteristically flat, a result of the ice sheets pressing the area down during glaciation. Photos: P. Forslund

1.2 The archipelago

An archipelago can be defined as an area situated on old bedrock which has been covered by ice and pressed down beneath sea level, from which it then rises (Fig. 1) (Jerling & Nordin, 2007). Hence, the archipelago coastline continuously shifts and moves towards the sea. This rather strict definition of an archipelago means that only a few of the world's island-rich areas can truly be called archipelagoes. Large archipelagos are rare, except for the one in the Baltic Sea, there are a few areas in north east North America, small areas around Greenland, west of Scotland and southern Chile which are also true archipelagos. The Stockholm archipelago, together with the archipelago off the west coast of Finland (frequently called the Archipelago Sea, as a collective name), constitutes one of the largest and most island-rich archipelago areas in the world (Jerling & Nordin, 2007; Ås *et al.*, 1997).

Evidence suggests that this area has been inhabited by humans since around 4,000 B.C. (Jerling & Nordin, 2007). Up to the beginning of the last century, most large islands were subjected to intense agricultural activities, and inhabitants usually combined farming with fishing (Ås *et al.*, 1997). However, most farming has now been abandoned, and as a consequence, islands which were previously kept open by grazing cattle are now being overgrown.

1.2.1 Main threats to coastal birds

Some of the main threats to biodiversity in the coastal zone include increased nutrient loads and habitat loss (Airoldi & Beck, 2007; Bonsdorff *et al.*, 1997). Shoreline property development, i.e. exploitation, in the area has increased tremendously (Sundblad & Bergström, 2014; Kindström & Aneer, 2007). Increased exploitation (new houses, bridges, piers, quays etc.) close to the shoreline has reduced the amount of suitable breeding habitats and good foraging habitats for many birds. This is possibly linked to reduced quality of fish reproduction habitats (Sundblad & Bergström, 2014; Sandström *et al.*, 2005) and reduced species richness of, e.g., fish (Eriksson *et al.*, 2004). In addition, boat tourism has increased in the last decades (Fig. 2) (Swedish Transport Agency, 2010) which probably has increased the disturbance to birds (e.g., Velando & Munilla, 2011; Bellefleur *et al.*, 2009).

Figure 2. During summer many tourists and holiday-makers use the archipelago for sailing. At the end of the day this is a common sight when boat travellers have found a safe place to spend the night in one of the many natural harbours in the archipelago. This poses a potential problem for birds nesting and foraging along the shoreline, since birds may be disturbed by humans. Photo: P. Forslund

1.3 Biodiversity

There are many formal definitions of biodiversity (DeLong, 1996), one of the more important being that of the Convention on Biological Diversity. This treaty was signed at the United Nations Conference on Environment and Development in Rio de Janeiro 1992. The Convention states that:

> 'Biological diversity' means the variability among living organisms from all sources including, *inter alia*[1], terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems. (Anon., 1992).

Biodiversity serves as a unifying concept since it includes all forms, levels and combinations of natural variation (Magurran & McGill, 2011; Gaston & Spicer, 2004). The definition itself is neutral, but the usage of the term 'biodiversity' is most often value laden (Gaston & Spicer, 2004).

The general building blocks of biodiversity can be divided into three groups: (i) genetic diversity; (ii) organismal diversity; and (iii) ecological diversity. Genetic diversity includes genetic components such as genes. Organismal diversity includes the taxonomic hierarchy and its components, such as species. Ecological diversity includes ecological differences between populations, habitats, ecosystems, landscapes and onwards (Gaston & Spicer, 2004).

1.3.1 Measuring biodiversity

For practical reasons, it can be useful to quantify biodiversity in one of various ways. A biodiversity measure which describes how biodiversity varies from one locality to another may be especially useful when evaluating the conservation value of an area or when prioritizing between different areas (Sarkar & Margules, 2002). So called biodiversity surrogates are often used as quantitative measures to stand in for overall biodiversity, which is more difficult to measure in its entirety. Traditionally, species richness (i.e. the number of species) has been used as a surrogate for biodiversity. However, using only a species richness metric does not capture differences in species composition between areas, which is one of the key features of biodiversity (Sarkar & Margules, 2002).

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[1] *Inter alia*, 'among other things'.

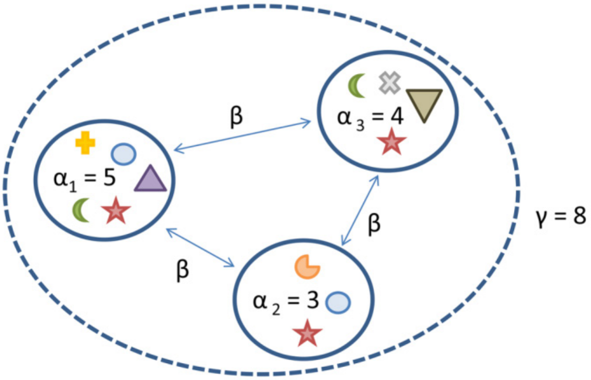

Figure 3. Biodiversity is often measured as species richness at three spatial scales: (i) α diversity, species richness within a site; (ii) β diversity, difference in species composition between sites; and (iii) γ diversity, the species richness of the whole landscape. Symbols refer to different species.

Species diversity consists of two components, richness and evenness. Species richness refers to the actual number of species within a site, and evenness refers to the proportions of the species present (Tuomisto, 2012; Magurran & McGill, 2011). A low evenness indicates that a site is dominated by few species. Biodiversity can be measured at several spatial scales (Whittaker, 1960). Alpha diversity (α) is the richness and evenness of individuals within a certain site, e.g., a habitat or an island. In Fig. 3, α diversity in site 1 is 5 species, for site 2 = 3 species and for site 3 = 4 species. Beta diversity (β) is the difference in species composition between sites. In Fig. 3, the greatest β diversity is between site 1 and 3, since only two species are shared, whereas five species are unique to the site where they occur. Gamma diversity (γ) is the species richness of a habitat or whole landscape (Magurran & McGill, 2011). In Fig. 3, the γ diversity is made up of eight species.

1.4 Conservation

Destruction, fragmentation and homogenization of habitats and natural landscapes have dramatically decreased biodiversity worldwide, and finding ways to mitigate this loss is a major concern (Butchart *et al.*, 2010). Since ancient times, humans have set aside areas in order to preserve different natural values, and reserves have been established during the last decades to protect biodiversity and to compensate for negative human impact (Margules & Pressey, 2000). However, since reserves comprise only a fraction of the total land area, land which is not protected has to be incorporated into conservation strategies to secure biodiversity in the long term (Bengtsson *et al.*, 2003). One example of such a strategy is the shore protection regulation in the Swedish Environmental Code (SFS, 2009).

1.4.1 Coastal bird conservation in Sweden

Population trends of coastal breeding birds in Sweden are fairly well known. Whereas some populations have increased, e.g., those of some gulls and terns, others have decreased, especially those of waders and diving ducks (Amcoff, 2012; Ottvall *et al.*, 2009). The reasons for these particular declines are not known, but invasive alien predators, habitat degradation and disturbance caused by humans are all factors known to negatively affect seabirds (Croxall *et al.*, 2012).

There are many bird sanctuaries in the Baltic Sea archipelago. Most of these areas are rather small and include one or two small islands. Further, coastal breeding birds are generally protected in the archipelago by the shore protection regulation (SFS, 2009). As the archipelago is home to some bird species which are found nowhere else in Sweden (Ottvall *et al.*, 2009; Svensson *et al.*, 1999), it is necessary to protect the breeding sites of these species if they are to be retained in the country.

Protected areas

Protecting areas represents an important strategy to reduce species extinction risks (Pimm *et al.*, 2014), with a global coverage of about 12% of the land area (Watson *et al.*, 2014).

There are a number of different types of protected areas in Sweden. They are all regulated by the Environmental Code (1998:808). The purpose of these protected areas is usually to protect valuable natural and cultural assets. In special protection areas, the right of access may be restricted, e.g., in wildlife sanctuaries (Fig. 4).

Animal and plant sanctuaries (Fig. 4) are established to protect animal or plant species in a certain area. Along the Swedish coast, animal sanctuaries are established for the purpose of protecting rare or disturbance-sensitive species. Animal sanctuaries consist of bird sanctuaries, which are established with the intention of protecting breeding birds, and seal sanctuaries, which are established to ensure that seals have undisturbed resting areas. Establishment is made by the County Administrative Boards and the municipalities based on chapter 7, 4–6 § in the Swedish Environmental Code. The general public, and sometimes even the land owner, is prohibited from visiting the specified area during a certain time of the year. The regulations often also cover the water surrounding the protected islands to varying degrees. The regulations can also restrict hunting and fishing rights (Statistics Sweden, 2014).

Figure 4. A sign showing that the island and surrounding waters are included in a bird sanctuary and that access therefore is prohibited. Photo: P. Forslund

Land or water areas may be designated as nature reserves by a County Administrative Board or municipality if this is necessary in order to preserve biological diversity, conserve valuable natural or cultural assets or to meet recreational needs in the area. In order for a nature reserve to be established, there must be a strong public interest in protecting the area. Nature reserves are the most common type of protected area in Sweden with more than 500 areas established in marine environments along the Swedish coastline. Their general conservation aims are usually broader than animal sanctuaries. Nature reserves are also formed by the County Administrative Boards and the municipalities with the support of chapter 7, 4–6 § in the Swedish Environmental Code, in order to protect biological diversity, protect or create valuable environments, protect or create environments for certain species, or meet human recreational needs. Each nature reserve has a management plan which regulates how the area shall be managed. The regulations of the management plan are largely determined by the aim of the reserve (Statistics Sweden, 2014).

The shore protection regulation

Swedish shorelines are a valuable natural asset with large biological diversity and stunning sceneries. The shore protection regulation and the public right of access to private land (*Allemansrätten*) make Sweden unique in an international perspective.

The Swedish shore protection regulation (SFS, 2009) was established in 1952 and prohibits new constructions within 100 m of the shoreline. The background was a realisation that access to shores was dwindling as a consequence of increasing shoreline exploitation, especially close to larger cities. The original purpose was mainly to guarantee continued access to lakes, sea and beautiful or unique unexploited nature for all citizens. Hence, the objective was not to protect these beautiful natural areas *per se* but to conserve them for the benefit of humans. In 1994, protection was also granted for plants and animals occurring at shorelines (Anon., 2001).

Sea-shores, as well as the shores of all lakes and watercourses, are protected from the shoreline and 100 m up on land and likewise 100 m out in the water. The County Administrative Boards may expand shore protection to 300 m (Anon., 2001). The shore protection regulation (SFS, 2009) has two purposes: (i) to assure public access to private land in the shore area and (ii) to maintain good living conditions for plant and animal species on land and in water. Thus, any new constructions, e.g., buildings or jetties, that "substantially alter the living conditions" for animals or plants are banned. Exemptions from shore protection may be granted if the exemption is motivated by at least one of six special circumstances (chapter 7, 18 c § in the Environmental Code of Sweden);

1. Already claimed areas
2. Physical isolation from the shore (e.g., by a road or railway)
3. Functional necessity of the object to be built
4. Need to expand some activity
5. Common interest
6. Some other prioritized interest.

Exemptions should normally not be granted in areas that are of particular importance for conservation or recreation and must not be granted if there are unacceptable impacts on biological assets (Anon., 2001). However, the problem is to assess at what temporal and spatial scales there will be an impact.

Despite the general protection, there is a gradual exploitation process where previously unspoiled shorelines are being exploited by a single jetty, only to have permission for more jetties being granted later (Sundblad & Bergström, 2014; Kindström & Aneer, 2007). As a results of this gradual process, termed the cumulative effects problem or the ‘tyranny of small decisions made singly’ (Theobald *et al.*, 1997), plants and animals are slowly being pushed back and eventually risk losing their habitats.

1.5 Birds as indicators

I have used coastal breeding birds as model organisms for measuring biodiversity. Although coastal birds are important to study in their own right, they are also useful model organisms for measuring biodiversity and can be used as indicators of the marine environment (Durant *et al.*, 2009), e.g., monitors of fish stocks (Furness & Camphuysen, 1997). Their ecology is comparatively well understood and they are both conspicuous and well-known to the general public and to decision makers (Ottvall *et al.*, 2009; Furness & Camphuysen, 1997). Birds also feed at a wide range of trophic levels and in a broad spectrum of coastal habitats – from the littoral to the open sea – thereby connecting marine and terrestrial environments (Durant *et al.*, 2009). A generalist can switch its food preference to match the relative abundance of prey items, whereas a specialist will be rapidly affected by any change in its main prey. Also, since trophic chains tend to be short in northern seas, the effects of changes in prey availability on birds are usually very rapid (Durant *et al.*, 2009). Hence, birds respond quickly to environmental changes. They are particularly suitable as indicators of environmental change in the archipelago since many bird species require specific shoreline habitats and access to sea. Compared to many other vertebrates, birds are easily counted by skilled observers and may also provide a means to explore responses to urban environments (Chace & Walsh, 2006).

The breeding success of coastal birds may decrease because of disturbance at nests or of small young (e.g., Finney *et al.*, 2005; Leseberg *et al.*, 2000). Coastal birds are therefore likely to be sensitive to perturbations in the environment caused by, e.g., habitat destruction or other changes in the ecological context, such as landscape changes or increased predation pressure. As many seabirds are predators, and consequently at high trophic level in marine food webs, they may also be used as indicators of pollution (Furness & Camphuysen, 1997).

2 Thesis aims

The general aim of this thesis is to investigate possible causes of spatial patterns of coastal breeding birds, and to what extent human activities and use of environmental legislation affect this diversity. Such knowledge is an important step towards a balance between maintaining biodiversity and making local human activities (e.g., settlements and recreation) possible. It is also required knowledge when establishing efficient conservation measures. The specific questions addressed in each paper were:

I What are the spatial distribution patterns of species richness (i.e. number of species within a 1 km^2 square) and compositional dissimilarity (i.e. differences in species composition between sites) of coastal breeding birds? How are these biodiversity measures related to large-scale environmental gradients?

II Are animal sanctuaries effective in capturing coastal breeding bird diversity compared to nature reserves and unprotected areas? Are hotspots (i.e. 1 km^2 squares with a high representation of uncommon species) overrepresented in animal sanctuaries?

III Does species richness and abundance of coastal breeding birds decrease as the degree of human shoreline exploitation (i.e. houses and jetties) increases?

IV To what extent are plans of new exploitation and bird diversity overlapping? To what extent has biodiversity been considered when exemptions to the shore protection regulation are granted?

3 Methods

3.1 Study area

The study area is situated in the Baltic Sea on the east coast of Sweden (Fig. 5). Papers I, II cover data collected in the counties of Uppsala, Stockholm and Södermanland, ranging from 58°36'N, 16°48'E in the south to 60°39'N, 17°33'E in the north. Paper III covers data collected in Uppsala and Stockholm, ranging from 58°44'N, 17°52'E in the south to 60°39'N, 17°33'E in the north. For paper IV, we used a subset of the data collected in Värmdö municipality, midpoint 59°17'N, 18°53'E, situated in the county of Stockholm.

The study area consists of a vast archipelago together with the adjacent mainland coast, and it includes more than 30,000 islands ranging from small and sparsely vegetated islets (<0.5 ha) to large and densely forested islands (up to 21,000 ha; Ås *et al.*, 1997). The archipelago belongs to the hemiboreal zone (Ahti *et al.*, 1968). The Baltic Sea is relatively young and has undergone several successional stages since the last glaciation. The water is brackish, with salinity varying between around 3.5‰ in the Bothnian Bay in the north to 7.0‰ in Skagerrak in the southwest. There are no tides, and the small fluctuations in water level are caused only by changes in atmospheric water pressure and winds. The archipelago in the northern Baltic Sea is one of the most island-rich archipelagos in the world, made up of tens of thousands of islands, and is a highly productive system (Ojaveer *et al.*, 2010; Heinänen *et al.*, 2008).

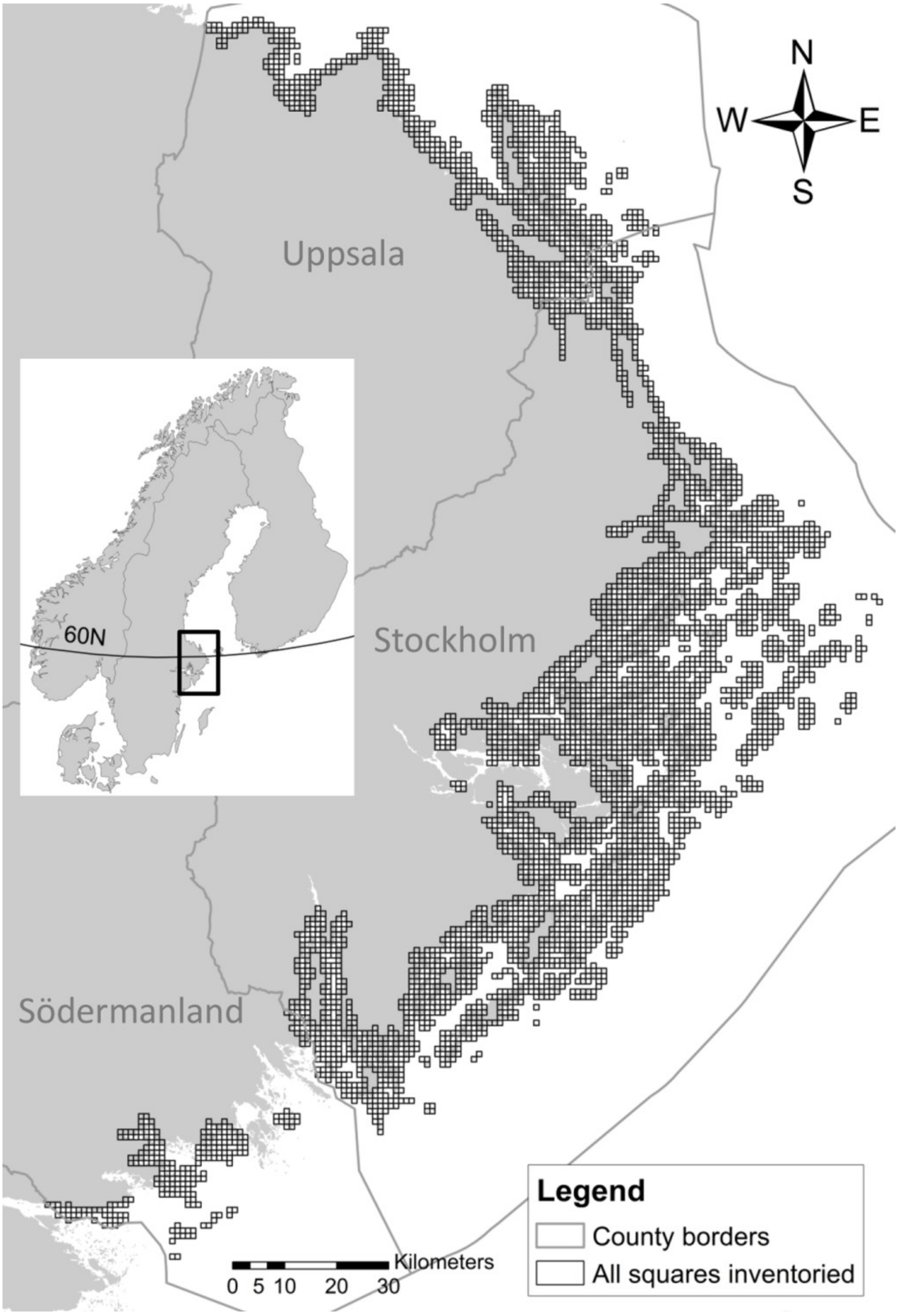

Figure 5. Map of Scandinavia and the study area with all 1 × 1 km squares (4,646 squares in total) in which coastal breeding birds were inventoried.

The post-glacial land uplift in the archipelago region is approximately 5 mm/year, which has resulted in environmental gradients both above (Ås *et al.*, 1997) and below (Bonsdorff & Blomqvist, 1993) the sea surface. This has contributed to the characteristic mosaic of different biotopes found in the archipelago. The land uplift has created a gradient where larger islands are found closer to the mainland and smaller islands (skerries) are found further out. Thus, there is a zonation of the archipelago, where the inner zone consists of larger islands which are generally less exposed to waves and winds. These larger islands are partially covered with forest, often contain settlements and have been greatly affected by agricultural activities. Typical tree species include pine *Pinus sylvestris*, spruce *Picea abies*, birch *Betula pubescens* and alder *Alnus glutinosa*. The middle and outer zones are characterized by small islands that are more exposed to waves and winds and often completely barren or sparsely vegetated. The smaller islands in the outer areas are typically vegetated by crowberry *Empetrum nigrum*, heather *Calluna vulgaris*, bushes (e.g., junipers *Juniperus communis*) and a few stunted trees (Ås *et al.*, 1997). It is widest in the central part and narrows at its northern and southern limits (Fig. 5).

The bird species breeding in this area are mainly those of coastal estuaries and mainland wetlands, and there are no true pelagic species. The area is characterised by strong seasonality, and most birds migrate south for the winter.

3.2 Bird inventory

The bird data used in this thesis were collected by the County Administrative Boards of Uppsala, Stockholm and Södermanland. The extensive inventories of coastal breeding birds in the study area were performed between the years of 2000 and 2004.

The 48 species included in the survey belong to ducks, waders, gulls, auks and one passerine (Rock Pipit, *Anthus petrosus*), which are species that to some extent are dependent on shoreline habitat for breeding (Table 1). The inventories were restricted to land within 100 m of the shoreline, and species records were summarised in squares of 1 × 1 km within the study area (Fig. 5). Squares were only included in the inventories if they comprised both land and water and had a minimum shoreline length of 25 m. In total, 4,646 squares were inventoried throughout the study area. Bird records from squares with a shoreline shorter than 25 m were assigned to the nearest square where breeding was possible, fulfilling the criteria of a shoreline longer than 25 m (N=126). Small islands may in some cases belong to two or more squares, and if it therefore proved difficult to separate the bird pairs to the respective square, all pairs were assigned to the square in which the largest part of the island was situated.

In order for the inventory of breeding pairs to be as accurate as possible, the inventory had to coincide with the start of the nesting period or, for some species, when chicks had hatched. Hence, inventories were carried out on three occasions, in April, May and June, so that birds with different breeding phenology could be observed. Thus, different species were recorded during the three different occasions. Ducks were inventoried before and during the species' normal egg laying period in the area, which is the period when the breeding pair or the male usually is resting off the breeding island. Species breeding in early spring were inventoried during the first occasion, in April, and species breeding in late spring were inventoried during the second occasion, in May. During the second occasion, Great Crested Grebe *Podiceps cristatus* and Eurasian Coot *Fulica atra* were inventoried through nest observations at the time of their nesting. Waders, gulls, auks and the Rock Pipit were inventoried in June, the third period, during the time of their nesting or shortly after their young had hatched (e.g., Great Cormorant *Phalacrocorax carbo sinensis*) (Fig. 6). The inventories were done by teams of two to three people on calm days without fog or rain. Each inventory team decided at what time of day they would perform the inventory. However, the instructions stated that the early morning hours (04–12 am) should be preferred.

Birds were recorded as breeding in a square based on a combination of observations of parental behaviour, birds seen on nearby water (April and May) and nests found on land (June). A requirement for assumed breeding was that presence of the species was recorded in the relevant time period for the species. On the first two occasions (April and May), the surveys were carried out entirely from open boats by cruising at low speeds around islands, so that shores were easily surveyed. Time spent inventorying was determined by the number of birds, the observers ability to overview all sections of the shoreline and so forth, but was approximately 20–40 min/km^2 during the first period (April) and usually 10–20 min/km^2 during the second period (May). Speed of the boat and distance to the shore was adjusted so that birds were not disturbed (minimum distance to the shore approximately 25 m). This was to avoid scaring birds and to keep them from taking flight, thus making them more difficult to count. On the third occasion (June) nest counts were conducted on land (Olsson, 2000).

Problems with detectability and systematic differences between sets of observations due to different teams of surveyors are both factors that may cause individuals or species to be overlooked (Rosenstock *et al.*, 2002). The design of the inventory did not allow for accounting for these possible sources of error in the analyses. However, all field workers were skilled bird watchers, using the same detailed inventory protocol in order to minimize systematic errors.

Figure 6. Great Cormorants *Phalacrocorax carbo sinensis* were inventoried during the third inventory period in June. A total of 6,945 breeding pairs were counted in the archipelago during the inventories. Photo: M. Nord.

3.2.1 Species groups and red-listed species

Based on the distribution maps from Svensson *et al.* (1999), all coastal breeding birds were classified into two species groups: specialist species and generalist species (Table 1). Specialist species (N=19) are species which breed exclusively in the coastal landscape, although a few have a disjunct distribution with occurrences also in restricted parts of the inland of northern Sweden (e.g., Velvet Scoter *Melanitta fusca*). Generalist species (N=29) are species breeding on the coast but also in inland wetlands, e.g., lakes or ponds (e.g., Mallard *Anas platyrhynchos*). As specialist species are confined to breeding in the archipelago, conservation actions in the area should preferably focus on them. Therefore, all papers included in this thesis have primarily focused on specialist species, but generalist species have also been considered.

Another group potentially requiring specific attention was that of red-listed coastal breeders (Sandström *et al.*, 2015). Paper I used the red-list of 2010 (Gärdenfors, 2010), while paper II used the red-list of 2015 (Sandström *et al.*, 2015). According to the 2010 red-list, there were seven red-listed species in each of the two groups. Four specialists and five generalists were classified as Near Threatened (NT), while three specialists and two generalists were classified as Vulnerable (VU). However, according to the 2015 red-list there were eight red-listed specialists (five NT and three VU). The Arctic Jaeger *Stercorarius parasiticus* was new on the red-list compared to 2010 (classified as NT). Common Sandpiper *Actitis hypoleucus* and Horned Grebe *Podiceps auritus* were no longer included on the red-list in 2015 compared to 2010, hence only five generalists were red-listed in 2015 (one NT and four VU).

Table 1. *List of names for the 48 coastal breeding bird species included in the inventory. Common names in English are given for each species as well as Latin and Swedish names. Each bird species was classified as either a specialist (i.e. species breeding exclusively in the archipelago area, N=19) or a generalist (i.e. species breeding in the archipelago but also in inland wetlands, N=29) based on distribution maps from Svensson et al. (1999).*

Common name	Latin name	Swedish name	Classification
Arctic Jaeger	*Stercorarius parasiticus*	Labb	Specialist
Arctic Tern	*Sterna paradisaea*	Silvertärna	Specialist
Barnacle Goose	*Branta leucopsis*	Vitkindad gås	Specialist
Black Guillemot	*Cepphus grylle*	Tobisgrissla	Specialist
Black-headed Gull	*Larus ridibundus*	Skrattmås	Generalist
Black-throated Diver	*Gavia arctica*	Storlom	Generalist
Canada Goose	*Branta canadensis*	Kanadagås	Generalist
Caspian Tern	*Hydroprogne caspia*	Skräntärna	Specialist
Common Eider	*Somateria mollissima*	Ejder	Specialist
Common Goldeneye	*Bucephala clangula*	Knipa	Generalist
Common Gull	*Larus canus*	Fiskmås	Generalist
Common Murre	*Uria aalge*	Sillgrissla	Specialist
Common Pochard	*Aythya ferina*	Brunand	Generalist
Common Redshank	*Tringa totanus*	Rödbena	Generalist
Common Ringed Plover	*Charadrius hiaticula*	Större strandpipare	Specialist
Common Sandpiper	*Actitis hypoleucus*	Drillsnäppa	Generalist
Common Shelduck	*Tadorna tadorna*	Gravand	Specialist
Common Teal	*Anas crecca*	Kricka	Generalist
Common Tern	*Sterna hirundo*	Fisktärna	Generalist
Eurasian Coot	*Fulica atra*	Sothöna	Generalist
Eurasian Curlew	*Numenius arquata*	Storspov	Generalist
Eurasian Oystercatcher	*Haematopus ostralegus*	Strandskata	Specialist
Eurasian Widgeon	*Anas penelope*	Bläsand	Generalist
Gadwall	*Anas strepera*	Snatterand	Generalist
Garganey	*Anas querquedula*	Årta	Generalist
Goosander	*Mergus merganser*	Storskrake	Generalist
Great Black-backed Gull	*Larus marinus*	Havstrut	Specialist
Great Cormorant	*Phalacrocorax carbo sinensis*	Storskarv	Specialist
Great Crested Grebe	*Podiceps cristatus*	Skäggdopping	Generalist
Greater Scaup	*Aythya marila*	Bergand	Specialist
Grey Heron	*Ardea cinerea*	Häger	Generalist
Greylag Goose	*Anser anser*	Grågås	Generalist
Herring Gull	*Larus argentatus*	Gråtrut	Generalist
Horned Grebe	*Podiceps auritus*	Svarthakedopping	Generalist

Common name	Latin name	Swedish name	Classification
Lesser Black-backed Gull	*Larus fuscus*	Silltrut	Specialist
Little Ringed Plover	*Charadrius dubius*	Mindre strandpipare	Generalist
Mallard	*Anas platyrhynchos*	Gräsand	Generalist
Mute Swan	*Cygnus olor*	Knölsvan	Generalist
Northern Lapwing	*Vanellus vanellus*	Tofsvipa	Generalist
Northern Pintail	*Anas acuta*	Stjärtand	Generalist
Northern Shoveler	*Anas clypeata*	Skedand	Generalist
Razorbill	*Alca torda*	Tordmule	Specialist
Red-breasted Merganser	*Mergus serrator*	Småskrake	Specialist
Red-necked Grebe	*Podiceps grisegena*	Gråhakedopping	Generalist
Rock Pipit	*Anthus petrosus*	Skärpiplärka	Specialist
Ruddy Turnstone	*Arenaria interpres*	Roskarl	Specialist
Tufted Duck	*Aythya fuligula*	Vigg	Generalist
Velvet Scoter	*Melanitta fusca*	Svärta	Specialist

3.3 Remote sensing data

3.3.1 Environmental characteristics

We investigated the effect of four environmental variables, all describing mainland and island physiognomic characteristics, on species richness and composition in paper I and controlled for these environmental variables in papers II–IV: distance to open sea, archipelago width, shoreline length and total land area within the square. Physiognomic characteristics such as these have previously been shown to be of importance for the occurrence of coastal breeding birds in archipelagos (von Numers, 1995). To get estimates of the different environmental variables for each square, GIS layers were used. These were obtained from the Topographical and General map, available through the Swedish Mapping, Cadastral and Land Registration Authority, and analysed using ArcMap 9.2 software (ArcGIS, ESRI, Redland, CA, USA).

Distance to open sea was calculated by delimiting a buffer line 150 m out from the outermost islands (i.e. the islands closest to the open sea), and then the Euclidean distance from the midpoint of each square to that buffer line was measured. Archipelago width was estimated for each square by adding the Euclidean distance from the square’s midpoint to the nearest mainland and to the distance to open sea. Shoreline length was calculated as the sum of all shorelines within each square, including both islands and mainland. The total amount of land area in each square was calculated by subtracting the water surface area in each square from the total area of the square (1 km^2). The remaining area was thus the above-water surface land area.

3.3.2 Protected areas

In paper II, two types of formally protected areas were studied: animal sanctuaries and nature reserves. The inventoried 1 × 1 km squares were classified into one of three categories based on the types of shorelines within each square:

- Unprotected squares (no length of shoreline belonging to a protected area, N=3,554)
- Nature reserve squares (≥5 m shoreline belonging to a nature reserve, N=877)
- Animal sanctuary squares (≥5 m shoreline belonging to an animal sanctuary, N=215)

Nature reserves and animal sanctuaries sometimes overlapped. Such squares, with shorelines belonging to both nature reserves and animal sanctuaries, were classified as animal sanctuaries (N=84), since animal sanctuaries is a stronger type of protection for birds.

3.3.3 Shoreline exploitation and exemptions

The index for human exploitation along shores, used in papers III and IV, focuses on the density of structures relating to anthropogenic physical modification within a buffer of 100 meters from the shoreline inwards land. It was based on two GIS layers developed by the County Administrative Boards in the region (Stockholm County Board, 2004), one layer for buildings and one for jetties (including quays, piers, marinas and boat houses extending into the water). These two layers were analysed using ArcMap 10.1 software (ArcGIS, ESRI, Redland, CA, USA).

The GIS layer displaying buildings was based on centroid points for individual buildings taken from the Swedish Property Map (Lantmäteriet, 2014). The GIS layer displaying jetties as point objects was made by the use of visual aerial photo interpretation, complemented with field controls (Stockholm County Board, 2004). In addition, densely populated areas (representing buildings) and small boat harbours larger than 0.25 ha (representing jetties) were included in the two layers, respectively, as polygons from the Property Map.

From the layers with point objects of buildings and jetties, maps with density of buildings or jetties were created by calculating the number of points within circles of 100 meter radius for each pixel (size 20 × 20 m) in a raster GIS. Based on this density (in brackets below), pixels were attributed to one of five exploitation classes:

Class 1: No exploitation (number of points/pixel in the layer of jetties: 0; number of points/pixel in the layer of buildings: 0)
Class 2: Weak exploitation (jetties: 1–2; buildings: 1–2)
Class 3: Marked exploitation (jetties: 3–4; buildings: 3–5)
Class 4: Strong exploitation (jetties: 5–7; buildings: 6–13)
Class 5: Very strong exploitation (jetties: >7; buildings: >13)

Polygons of densely populated areas and small boat harbours from the Property Map, within the buffer of 100 m from the shoreline, were then added to the layers and attributed to class 5 ('Very strong exploitation').

For each square, a weighted average was calculated based on the percentage area occupied by each exploitation class (classes 1–5 of 'exploitation') in each square. Because the correlation between the exploitation index for buildings and jetties was very high (0.92), they were combined into a single variable, called 'exploitation', by giving each square the highest of the weighted averages for either buildings or jetties. This was done to cover the full degree of human exploitation of shorelines within each square.

For paper IV, we reviewed public documents regarding applications for exemption from the shore protection regulation within the administrative area of Värmdö municipality. The documents covered the period of 1 January 2011 to 31 May 2012; dates refer to when cases were first started. In total, 403 applications were retrieved. From the documents, information was compiled about geographical location (to enable connection to the bird inventory data) and decision made (whether the exemption was granted or not granted). Specialist administrative officers at the municipality office dealt with and decided about 362 of the applications. However, when the recommendation was to reject the application, the cases (N=41) were referred to the Building, Environment and Health Committee for decision, which has members from the political parties. For a more detailed analysis, more information was acquired for a subset (N=42) of the cases dealt with by administrative officers and nearly all cases (39 out of 41 cases; detailed information was missing for 2 cases) dealt with by the political committee. For all these 81 (=42+39) cases, information was compiled about whether the application concerned a planned construction or was made in retrospect, whether assessments had been made on the consequences for biodiversity and public access to shores, the areal extent of the shore protection at the site in question (i.e. 100 or 300 m), and whether 'already claimed for exploitation' was given as a special circumstance for granting the application.

3.4 Beta diversity

In paper I, we wanted to explore species composition, in the form of β diversity. Based on Anderson *et al.* (2011) we chose to use a turnover type of β diversity (Fig. 7). The idea with a turnover β is to measure the change in community composition from one square to another along, e.g., an environmental gradient such as distance to open sea.

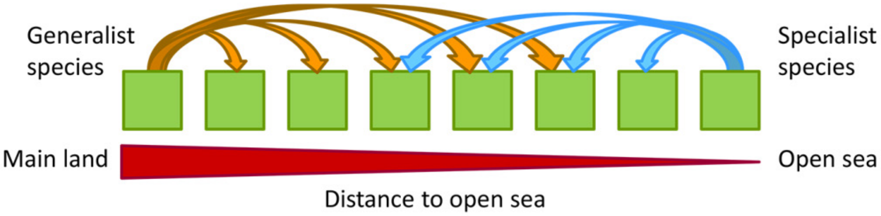

Figure 7. This figure illustrates the essential idea with a turnover β diversity, as it measures the change in community composition, e.g., change in the identity and/or cover of individual species, from one square to another along the environmental gradient of distance to open sea. Green squares are sampled squares and the red arrow illustrates where along the gradient of distance to open sea the square is situated. The orange and blue arrows represent how individual species within the groups of generalist and specialist species may replace each other, i.e. the turnover of species composition along the gradient. There may be a similar number of species found in every square along the gradient but the species composition will be different as the species identities change when moving from main land to open sea.

However, estimates of β diversity can be affected by changes in the number of species or the α diversity (Anderson *et al.*, 2013; Chase *et al.*, 2011; Vellend *et al.*, 2007). Hence, large β diversity estimates may be caused by ecological differences between squares which generate different community composition, but it may also be a result of differences in α diversity between those sites. In order to draw relevant conclusions from β diversity analysis it is therefore necessary to account for this α-driven component (Anderson *et al.*, 2011; Chase *et al.*, 2011; Kraft *et al.*, 2011). Thus, we not only analysed β diversity using the classical Sørensen’s dissimilarity index, but also by using the probabilistic Raup-Crick measure (Raup & Crick, 1979).

For each pair of squares, Sørensen’s dissimilarity index was calculated as:

$$\beta_S = 1 - \frac{2w}{(a+b)}$$

where a and b are the numbers of species in each plot of two samples, and w is the number of shared species (Magurran & McGill, 2011). We calculated the Raup-Crick estimate (β_{RC}) (Anderson *et al.*, 2011; Chase *et al.*, 2011; Raup & Crick, 1979) by following the protocol of Chase *et al.* (2011).

3.5 Hotspots

In paper II we wanted to investigate the overlap between so called hotspots of specialist species and protected areas. A scoring method called the rarity weighted richness index (RWRI) was used to identify hotspot squares (Williams *et al.*, 1996). This index has previously been shown to perform well, even compared to more complex methods (Albuquerque & Beier, 2015; Csuti *et al.*, 1997). Within each 1 × 1 km square, each specialist species was assigned a weight based on the inverse of the number of squares the species occupied, following Williams *et al.* (1996), thus putting more emphasize on rare species (Greenwald & Bradley, 2008; Williams *et al.*, 1996). The RWRI-score was calculated as:

$$\mathrm{RWRI} = \sum_{\substack{i:c_i \neq 0, \\ 1 \leq i \leq n}} (1/c_i)$$

where c_i is the number of squares occupied by species i. As a sensitivity test, four RWRI-score cut-off values were compared; 100%, 75%, 50% and 20%.

4 Results and Discussion

Common Eider *Somateria mollissima* was by far the most common bird species found, both in terms of squares with occurrence (3,163 squares, out of a total of 4,646) and to number of breeding pairs (111,007 breeding pairs). Other dominant species were Goosander *Mergus merganser*, which was found in 2,642 squares, Common Gull *Larus canus* found in 2,453 squares, Mallard *Anas platyrhynchos* found in 2,085 squares, and Mute Swan *Cygnus olor* found in 1,964 squares. Greater Scaup *Aythya marila*, Little Ringed Plover *Charadrius dubius*, and Red-necked Grebe *Podiceps grisegena* were all rare species which only occurred in 2 squares with just 2 breeding pairs present in the entire study area.

Some colony-nesting bird species had large numbers of breeding pairs recorded but had aggregated occurrences. Such species included Herring Gull *Larus argentatus* with 9,291 breeding pairs in 721 squares, Arctic Tern *Sterna paradisaea* with 8,432 breeding pairs in 1,156 squares, and Razorbill *Alca torda* with 7,835 breeding pairs in 96 squares.

The number of coastal specialists found per square throughout the entire study area ranged between 0 and 13 (median=2; quartiles=1 and 3), and the number of coastal generalists found ranged between 0 and 15 (median=3; quartiles=2 and 6). Specialist species tended to be more abundant in squares closer to open sea, whereas generalists had a more uniform distribution with a tendency to be more abundant in squares closer to mainland, i.e. further from open sea (Paper I, Fig. 8).

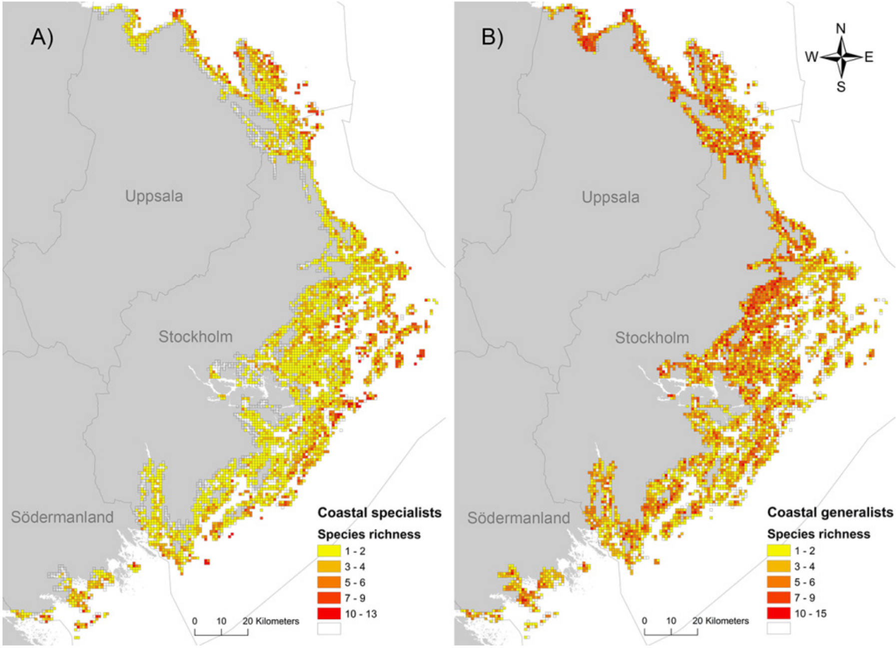

Figure 8. Patterns of observed species richness per square for (A) coastal specialist species (N=19), and (B) generalist species (N=29). In total 4,646 squares was inventoried throughout the counties of Uppsala, Stockholm and Södermanland.

4.1 Environmental variables

4.1.1 Alpha diversity

The effect of the environmental variables on bird species richness, i.e. distance to open sea, land area, shoreline length and archipelago width, was the main focus of paper I, but these environmental variables were also included in papers II–IV, since we wanted to control for them in those studies.

Distance to open sea had opposite effect on specialists and generalists (Papers I–IV, Figs. 8 & 9). The number of specialist species per square, i.e. α diversity, decreased with increasing distance to open sea, while the number of generalist species increased with increasing distance to open sea, i.e. closer to mainland. Specialist species were also found breeding in narrow parts of the archipelago, close to the mainland. Hence, the preference for breeding sites close to open sea was irrespective of archipelago width (Fig. 8A). This is in agreement with previous work in the Baltic Sea region, which has shown that many species which we classified as specialists prefer islands with little or no vegetation (Heinänen & von Numers, 2009; Heinänen *et al.*, 2008; Rönkä *et al.*, 2008; von Numers, 1995), which are especially common in localities close to open sea exposed to wind and waves (Ås *et al.*, 1997). Furthermore, these areas probably offer high-quality foraging areas in the near vicinity, and specialised feeders may be dependent on breeding close to these foraging areas (Rönkä *et al.*, 2008; Hildén, 1965). High predation risks, e.g., due to the presence of mustelids and corvids, closer to the mainland could be another reason for specialist species to prefer breeding sites close to open sea (Ahlén & Andersson, 1970). However, if predation was a major factor affecting the distribution of specialist species, these species should be absent in narrow parts of the archipelago, but this was not the case (Fig. 8A). The observed preference of generalist species to breed closer to mainland is similar to findings from the Finnish archipelago (von Numers, 1995), and also agrees with the general freshwater ecology of generalist species. Islands close to mainland tend to be large with tall vegetation, and the water is more brackish there than further out in the archipelago. Thus, the characteristics of the inner archipelago are more similar to mainland freshwater lakes (Ås *et al.*, 1997).

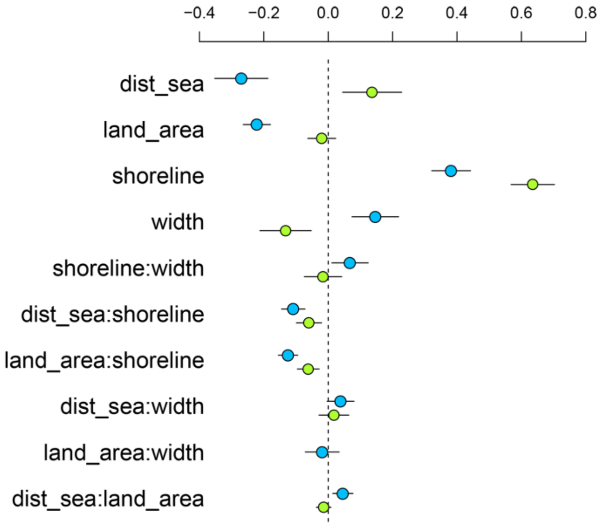

Figure 9. Parameter estimates and 95% confidence intervals for specialist coastal breeders, **blue** circles, and generalist coastal breeders, **green** circles. The generalized linear mixed models (GLMM) used data on environmental gradients to investigate the effect on the number of species per square. For generalist species, the interaction between land area and archipelago width was removed due to convergence problems. Land_area = land area within each square; dist_sea = distance to open sea; shoreline = total shoreline length in each square; width = archipelago width. Interactions between variables are indicated by ':'.

As most coastal species breed close to water, the number of species of both specialists and generalists increased with increasing shoreline length, probably as a result of species-habitat area relationships. However, the interactions showed that the effect of shoreline length was dependent on land area in the square (Paper I, Fig. 9). Hence, there were fewer specialist species in squares with large land areas, even with long shorelines (Paper I), suggesting that shoreline habitat was less suitable for specialist species in squares with larger land area than in squares with smaller land area. Islands with a small land area may, in comparison to larger islands, be flatter, more open and have lower vegetation. Such features have been found to be attractive to coastal specialist species in the nearby Finnish archipelago (Rönkä *et al.*, 2008), and are highly likely to be similar in our study area as well. However, for generalist species the shoreline effect was only slightly influenced by land area (Paper I). The main effect of land area was negative for both species groups in paper II–IV, i.e. the number of species decreased as land area increased, but there was no significant effect on generalists in paper I (Fig. 9). Archipelago width affected specialist and generalist species differently: the number of specialist species increased with increasing archipelago width, while generalist species showed the opposite pattern (Paper I–III, Fig. 8). However, in paper IV archipelago width was positively associated to the number of both specialist and generalist species. This may be due to that the archipelago width was not very variable in the Värmdö study area (Paper IV).

The breeding bird fauna of archipelagos differs from that of other coastal areas in being highly dependent on island qualities, with differences in shore environments as a main driver (Heinänen & von Numers, 2009). This was also apparent since we found that the number of species strongly increased as total shoreline length increased in all papers. The number of specialist species increased with distance from mainland, which is likely explained by good access to suitable breeding habitats (mostly low, flat rocky shores) and the comparatively limited degree of exploitation in this outer region (Paper III and IV). Overall, the environmental variables had larger parameter estimates in models explaining species richness than had protection category (Paper II) or shoreline exploitation (Paper III). This point to archipelago landscape characteristics being the main drivers of bird richness.

4.1.2 Beta diversity

The different effects which we found of distance to open sea, land area and archipelago width on specialists and generalists suggest a turnover of species when moving along these environmental gradients (i.e. from close to mainland towards open sea).

Differences in community composition (measured as both β_S and β_{RC}) between squares within the specialist and generalist species groups were primarily driven by differences in land area and distance to open sea (Paper I,

Fig. 10). Species turnover is usually stronger the steeper the environmental gradient (Kessler *et al.*, 2009), and it is often related to habitat heterogeneity (Veech & Crist, 2007). Further, differences in community composition are often a consequence of spatial variation in habitat, especially for birds (Reif *et al.*, 2008; Veech & Crist, 2007; Mac Nally *et al.*, 2004; Brown *et al.*, 1995). However, land area and distance to open sea were unlikely drivers of community composition, *per se*, but rather proxies for other factors that determine the presence of different species. For example, a large land area in a particular square is often due to the presence of large islands, which tend to be more covered by vegetation compared to small islands (Rönkä *et al.*, 2008). Hence, such habitat heterogeneity likely promotes and maintains spatial β diversity patterns in the archipelago (Suurkuukka *et al.*, 2012; Freestone & Inouye, 2006; Loreau, 2000).

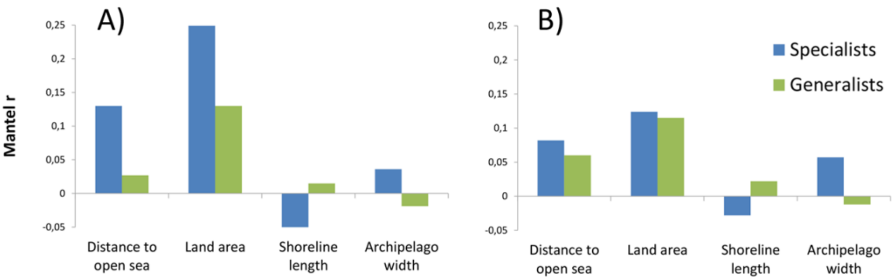

Figure 10. Magnitude of the correlation coefficients between differences in coastal breeding bird communities and differences in environmental variables. Bars represent *r* values, estimated by partial Mantel test, which are the correlations of A) Sørensen's dissimilarity index (β_S) or B) the probabilistic Raup-Crick measure (β_{RC}) with the distance matrices for the explanatory variables.

4.2 Effectiveness of protected areas

4.2.1 Species richness and abundance

In paper II, we show that animal sanctuaries (N=215) were significantly more effective in capturing species richness, while nature reserves (N=877) were less effective, than unprotected squares (N=3,554) regarding specialist species as well as red-listed specialist species (Table 2).

Further, more than half of the species had a significantly higher average number of breeding pairs in animal sanctuaries than in unprotected squares (N=26). Also, rare specialist species were more concentrated to animal sanctuaries than common specialist species were.

Table 2. *Number of breeding specialist, generalist and red-listed specialist bird species per square in relation to protection category and environmental variables. Unprotected squares form the baseline which the other categories are compared to. Protection categories are shown in bold.*

	Specialists		Generalists		Red-listed specialists*	
	Estimate	*P*-value	Estimate	*P*-value	Estimate	*P*-value
Intercept	2.6439	<0.001	1.3039	<0.001	-0.1812	<0.001
Animal sanctuary	**0.0711**	**<0.001**	**0.1432**	**0.0035**	**0.2299**	**<0.001**
Nature reserve	**-0.0317**	**<0.001**	**-0.0407**	**0.1784**	**-0.1466**	**<0.001**
Distance to sea	-0.2515	<0.001	0.1070	<0.001	-0.3062	<0.001
Land area	-0.0969	<0.001	-0.0862	<0.001	-0.5239	<0.001
Shoreline length	0.0423	<0.001	0.3227	<0.001	0.1480	<0.001
Archipelago with	0.1139	<0.001	-0.1130	<0.001	0.2040	<0.001

*Spatial autocorrelation has not been taken into account in the model for red-listed specialist species, because of convergence problems.

Gaston *et al.* (2008) argue that increased protected area effectiveness can be achieved by protection in places of high species richness or high abundance of certain species. For example, Common Murre *Uria aalge* and Razorbill have breeding populations highly aggregated to certain islands. Hence, many such islands have since long been protected in order to secure the long-term survival of these species. The fact that animal sanctuaries still manage to capture species of conservation concern, even though some areas were established some 30 years prior to the bird inventory, indicate limited spatial dynamics for some species. Protected areas can also be effective because the protected areas, although originally maybe not having higher species richness than unprotected areas, have had lower levels of threats (Gaston *et al.*, 2008). The County Administrative Boards have, e.g., imposed regulations that prohibit humans from entering some animal sanctuaries during the breeding season. This may have contributed to increased species richness and abundance of species that prefer to nest in undisturbed areas, perhaps due to a redistribution of birds from other areas into undisturbed areas.

4.2.2 Identifying bird diversity hotspots

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 (Fig. 11).

The RWRI index showed that hotspots had a mosaic distribution throughout the whole archipelago and that many of them still lacked protection (Fig. 11). Therefore, the rarity-index may be useful to identify potential gaps in the protected area network. Conversely, since hotspots also were situated in unprotected areas, this may suggest that birds breed in suitable areas regardless of protection status. If this is the case, further protection may not be needed. If no new animal sanctuaries are established, the future management of unprotected shorelines will be very important for future bird conservation. Nevertheless, most animal sanctuaries were small and scattered throughout the archipelago. Therefore, any potential future animal sanctuaries may be rather small and still function as sanctuaries for many species.

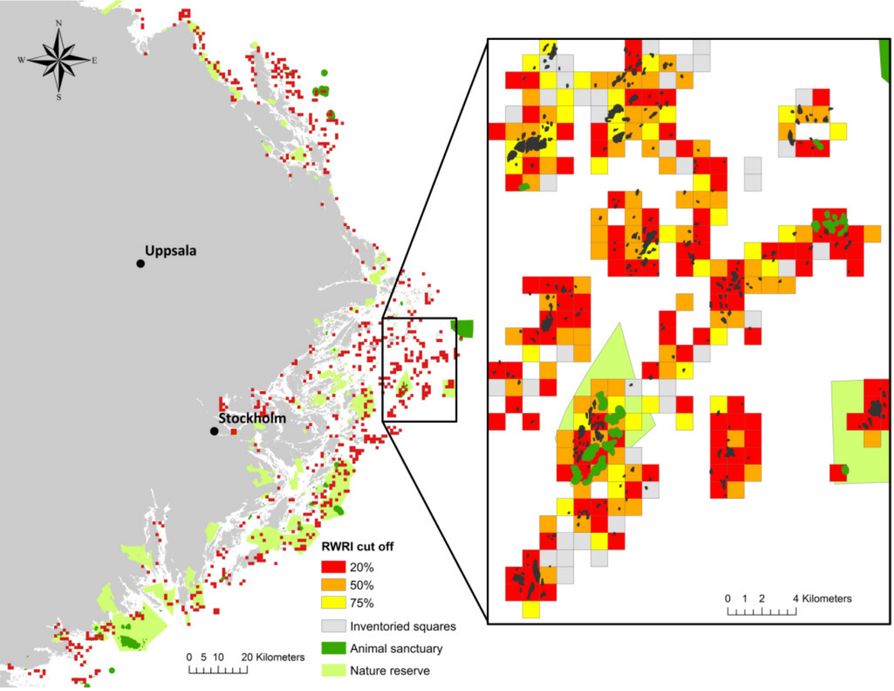

Figure 11. Classification of squares based on the rarity weighted richness index (RWRI), i.e. the hotspot analysis. At higher cut-off values, i.e. 20% (red) and 50% (orange), rare species are more important since they have a higher weight assign to them.

4.3 Shoreline exploitation

4.3.1 Exploitation index and exemptions

The degree of exploitation was found to increase with increasing distance to open sea (Paper III). Likewise, applications for exemptions from the general shore protection regulation in the Värmdö municipality were also more likely to be granted close to previously exploited areas (Paper IV, Fig. 12). Degree of exploitation and the likelihood for applications for exemptions to occur both increased significantly with increasing shoreline length (Paper III and IV). These results are in line with those of Sundblad and Bergström (2014), who found a large relative increase in development rate for shorelines which already were exploited to some degree.

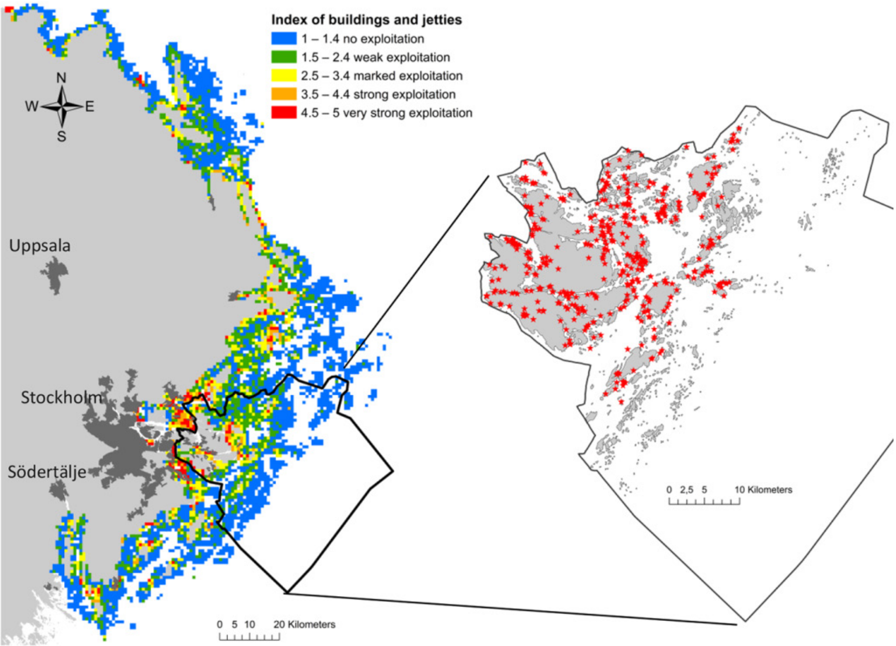

Figure 12. The combined weighted index of buildings and jetties (to the left) shows that the zone closest to open sea is comparatively unexploited (blue), while inner parts are more exploited (orange and red). The area outlined and shown to the left is the municipality of Värmdö, where applications for exemptions from the shore protection regulation are shown as red stars.

Applications for exemptions were common, and an overwhelming amount of the applications for exemptions were granted (96%, N=403), despite a lack of site-specific data on biodiversity. A common statement in the reasons given for granting exemptions was that the planned exploitation will not impair the living conditions for animals and plants. However, according to the public documents, only a minority of the cases presented information on site-specific knowledge. The information referred to was a habitat model of fish recruitment (Bergström *et al.*, 2007) and terrestrial inventories showing high conservation values. Interestingly, in most cases where site-specific knowledge was present the applications were rejected, meaning that most granted cases used no site-specific information. Indicating most applications are granted without specific knowledge of the animals and plants present at a particular site, which is a problem that is not unique to Sweden (Reed *et al.*, 2014; Rissman *et al.*, 2007).

4.3.2 Effects on coastal bird richness

In paper III, we found that the number of specialist and generalist species were differently affected by the degree of shoreline exploitation (Fig. 13). Species richness of specialist species decreased as human shoreline exploitation increased. However, no distinct effect of shoreline exploitation on generalist species richness was found. Similarly, in paper IV, we found that the probability of applications for exemptions from the general shore protection regulation to occur was higher in squares with fewer specialist species. Negative relationships (mainly for coastal specialist species, Fig. 13) may be due to specialist species and humans having different habitat preferences, or that human disturbance causes specialist species to avoid exploited areas. Positive correlations between human exploitation and coastal birds may be caused by humans and birds (mainly generalist species) sharing original habitat preferences. Possible mechanisms explaining the relationships that we found in paper III and IV are discussed below.

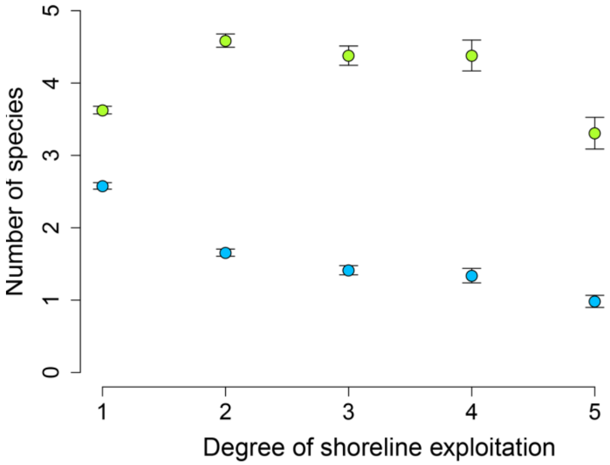

Figure 13. Number of species found, with 95% confidence intervals, for specialist coastal breeders, **blue** circles, and generalist coastal breeders, **green** circles. N_1=2,528; N_2=990; N_3=512; N_4=188 and N_5=175.

Habitat preferences

Similar or dissimilar original habitat preferences of humans and birds will cause either positive or negative relationships between human shoreline exploitation and bird diversity. For example, many coastal specialist species have a strong preference for exposed shorelines close to open sea (Fig. 8A) (Heinänen *et al.*, 2012; Heinänen *et al.*, 2008), whereas humans generally choose shorelines which are less exposed and thus located closer to the mainland (Fig. 12). Hence, the negative effect of human exploitation on specialist species richness could be explained by large scale geographic distribution of humans and coastal birds. The results in paper III indicated that the most likely explanation was either that many coastal species avoided humans or that in the mid and outer archipelago birds mainly prefer exposed shorelines, while humans mainly prefer sheltered ones.

Changes in food availability

Shoreline exploitation may also affect the birds directly, via food availability for many species through food addition, changes in vegetation types and structures of the habitat, or indirectly, if the predation risk increases due to disturbance and predators. The most obvious examples of food addition are gulls eating human waste and leftovers from fishing (e.g., Pap *et al.*, 2013; Meager *et al.*, 2012; Campbell, 2008) and grazing birds (geese and ducks) that use the good grazing grounds of lawns (Campbell, 2008; Traut & Hostetler, 2004). Sundblad and Bergström (2014), showed that shoreline exploitation of jetties in the Stockholm archipelago degraded the spawning grounds for fish, causing reductions in the production of fish recruits, thus the habitat for fish-eating bird species may also be degraded. However, we found no support for any of these scenarios in our analyses.

Changed predation

Further, predation risks have been suggested to be either higher (Sorace, 2002; Leseberg *et al.*, 2000) and lower (Brzezinski *et al.*, 2012) in exploited areas. Predation by mink is often mentioned, since mink has been documented to dramatically change the distribution of coastal breeding birds in this and other archipelagos in the Baltic (Roos & Amcoff, 2011; Nordström *et al.*, 2004). However, mink are often observed on islands regardless of degree of human exploitation (Roos & Amcoff, 2011), likely because they are good swimmers and widespread in the archipelago. None of our results suggests either increased or reduced predation risk.

Human disturbance

Human disturbance in areas with abundant food or close to nests may reduce foraging success and food provisioning rates to young birds (Sabine *et al.*, 2008; Leseberg *et al.*, 2000). Similarly, human disturbance at nesting sites during the period when birds take care of the brood, may increase the risk of predation of eggs or nestlings, since adult birds temporarily leave their nests or young unattended (Tjorve & Underhill, 2008; Bolduc & Guillemette, 2003). Previous studies suggest that there is interspecific variation in how species tolerate humans (Laursen *et al.*, 2005) and that habituation to the presence of humans may reduce the effects of human disturbance (Pap *et al.*, 2013; Severcan & Yamaç, 2011). Interestingly, several generalist species have been reported to be less sensitive to human exploitation (e.g., Common Gull, Mallard and Black-headed Gull *Larus ridibundus*) (Pap *et al.*, 2013). This may possibly be a contributing factor for the lack of any strong negative relationships between richness of generalist species and the degree of human exploitation.

An explanation to the negative relationship between probability of application and the number of specialist species in paper IV may be that previous exploitation has caused specialist species to disappear due to disturbance. However, this is also where new exploitation is most likely to occur (Paper IV). This may mean that as the degree of exploitation increases (see also Sundblad & Bergström, 2014), so will the negative effects of exploitation on birds. Such a continuous but slow process is difficult to investigate, and cannot be revealed by short-term snap-shot data (e.g., Paper III; Wood *et al.*, 2015). This is generally known as the cumulative effects problem or the 'tyranny of small decisions made singly' (Theobald *et al.*, 1997).

5 Conclusions and implications for conservation

The aim of this thesis was to explain spatial patterns of coastal breeding birds using ecological factors, human shoreline exploitation and conservation actions in the form of protected areas. Based on the results in this thesis, it is clear that spatial patterns of coastal breeding birds, especially specialist species, are highly affected by these factors.

Some important conclusions and summarized answers to the questions in thesis aims are:

- **Long shorelines are of great importance for species richness**
  Shorelines were found to be positively associated with species richness in all four papers, i.e., species richness of both specialist and generalist species increased as shoreline length increased. However, long shorelines in combination with large land areas had a negative effect on species richness of specialists. Distance to open sea had opposing effects on specialists and generalists. Further, there were complex interactions. These results are directly applicable when establishing new bird sanctuaries (i.e. deciding which environmental variables to prioritize) and in evaluating exemptions from the shore protection regulation (i.e. since presence of species of conservation concern are linked to environmental variables). Small land areas with long shorelines are highly valuable both for species richness in general and for red-listed species in particular, and such areas should therefore be prioritized in conservation planning.

- **Animal sanctuaries were significantly more effective in capturing specialist species richness than unprotected areas, while nature reserves were less effective than unprotected areas**

Animal sanctuaries captured both abundance and species richness of coastal breeding birds of conservation concern (i.e. specialist species as well as red-listed species). Animal sanctuaries were also better in capturing hotspots of bird diversity compared to both nature reserves and unprotected areas. However, many specialist species have large proportions of their populations in areas that are currently unprotected. Therefore, relevant management of unprotected shorelines is essential. Further, since reserve selection needs to be based on a systematic approach with well-defined targets, the results suggest that a rarity-index may be a valuable and useful tool for identifying candidate sites.

- **Specialist species richness decreased as human shoreline exploitation increased**
  Shoreline exploitation had different effects on the number of specialist species and generalist species. Specialist species decreased with increasing exploitation, while there was no significant effect of increases in shoreline exploitation on species richness of generalist species. The negative relationships found may be caused by differences in original habitat preferences and an avoidance of human disturbance. The results further emphasize the need to protect the shoreline against further exploitation and to provide guidance for authorities in their work with handling applications for new building sites.

- **The proportion of granted exemptions from the shore protection regulation was 96%**
  Granted applications for exemptions most often occurred close to already exploited areas, and the occurrence of applications was negatively related to the number of specialist species. The effect on biodiversity was often assessed, but references to specific information on biodiversity were rare. However, when specific information was available, the application was usually rejected. This implies that if more specific information was available, perhaps more applications would be rejected since the impact on biodiversity could be more fully assessed. Furthermore, this emphasizes that there is a clear need for repeated inventories of both changes in the degree of exploitation and in bird diversity in order to identify and consider exploitation effects on birds and other organisms for future implementation of shore protection by authorities.

A future development of this work would be to collect and analyse time-series data on birds and shoreline exploitation, for example to compare bird communities before and after protection or exploitation. Also, mapping more fine scale habitat characteristics, e.g., different shore types and water depth, may provide more accurate knowledge about mechanisms that determine species diversity.

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References

Ahlén, I. & Andersson, Å. (1970). Breeding ecology of an eider population on Spitsbergen. *Ornis Scandinavica*, pp. 83-106.

Ahti, T., Hamet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici,* 5(3), pp. 168-211.

Airoldi, L. & Beck, M.W. (2007). Loss, status and trends for coastal marine habitats of Europe. In: Gibson, R.N., Atkinson, R.J.A. & Gordon, J.D.M. (eds) *Oceanography and Marine Biology: An annual review,* 45, pp. 345-405.

Albuquerque, F. & Beier, P. (2015). Rarity-weighted richness: a simple and reliable alternative to integer programming and heuristic algorithms for minimum set and maximum coverage problems in conservation planning. *Plos One,* 10(3), e0119905.

Amcoff, M. (2012). Ejdern minskar, nästan inga ungar i år. Upplandsstiftelsen. Pressmeddelande. [in Swedish]

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S. & Davies, K.F. (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters,* 14(1), pp. 19-28.

Anderson, M.J., Tolimieri, N. & Millar, R.B. (2013). Beta diversity of demersal fish assemblages in the north-eastern pacific: interactions of latitude and depth. *Plos One,* 8(3), e57918.

Anon. (1992). Convention on Biological Diversity 1760 UNTS 79; 31 ILM 818. United Nations Environment Programme.

Anon. (2001). The Swedish environmental code. A résumé of the text on the Code and related Ordinances. Regeringskansliet. Ministry of the Environment.

Bellefleur, D., Lee, P. & Ronconi, R.A. (2009). The impact of recreational boat traffic on marbled murrelets (*Brachyramphus marmoratus*). *Journal of Environmental Management,* 90(1), pp. 531-538.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nyström, M. (2003). Reserves, resilience and dynamic landscapes. *Ambio,* 32(6), pp. 389-396.

Bergström, U., Sandström, A. & Sundblad, G. (2007). Fish habitat modelling in the Baltic Sea archipelago region. *Balance Interim Report,* 11.

Bolduc, F. & Guillemette, M. (2003). Human disturbance and nesting success of Common Eiders: interaction between visitors and gulls. *Biological Conservation,* 110(1), pp. 77-83.

Bonsdorff, E. & Blomqvist, E.M. (1993). Biotic couplings on shallow water soft bottoms - examples from the northern Baltic Sea. *Oceanography and Marine Biology an Annual Review,* 31, pp. 153-176.

Bonsdorff, E., Blomqvist, E.M., Mattila, J. & Norkko, A. (1997). Coastal eutrophication: causes, consequences and perspectives in the Archipelago areas of the northern Baltic Sea. *Estuarine Coastal and Shelf Science,* 44, pp. 63-72.

Brook, B.W., Sodhi, N.S. & Ng, P.K.L. (2003). Catastrophic extinctions follow deforestation in Singapore. *Nature,* 424(6947), pp. 420-426.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995). Spatial variation in abundance. *Ecology,* 76(7), pp. 2028-2043.

Brzezinski, M., Natorff, M., Zalewski, A. & Zmihorski, M. (2012). Numerical and behavioral responses of waterfowl to the invasive American mink: a conservation paradox. *Biological Conservation,* 147(1), pp. 68-78.

Butchart, S.H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P., Almond, R.E., Baillie, J.E., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnick, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C. & Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science,* 328(5982), pp. 1164-1168.

Campbell, M.O.N. (2008). The impact of vegetation, river, and urban features on waterbird ecology in Glasgow, Scotland. *Journal of Coastal Research,* 24(3), pp. 239-245.

Chace, J.F. & Walsh, J.J. (2006). Urban effects on native avifauna: a review. *Landscape and Urban Planning,* 74(1), pp. 46-69.

Chase, J.M., Kraft, N.J., Smith, K.G., Vellend, M. & Inouye, B.D. (2011). Using null models to disentangle variation in community dissimilarity from variation in α-diversity. *Ecosphere,* 2(2), art24.

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A. & Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International,* 22(1), pp. 1-34.

Csuti, B., Polasky, S., Williams, P.H., Pressey, R.L., Camm, J.D., Kershaw, M., Kiester, A.R., Downs, B., Hamilton, R. & Huso, M. (1997). A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation,* 80(1), pp. 83-97.

DeLong, D.C. (1996). Defining biodiversity. *Wildlife Society Bulletin*, 24(4), pp. 738-749.

Durant, J.M., Hjermann, D.Ø., Frederiksen, M., Charrassin, J.-B., Le Maho, Y., Sabarros, P.S., Crawford, R.J. & Stenseth, N.C. (2009). Pros and cons of using seabirds as ecological indicators. *Climate Research*, 39, pp. 115-129.

Eriksson, B.K., Sandström, A., Isaeus, M., Schreiber, H. & Karas, P. (2004). Effects of boating activities on aquatic vegetation in the Stockholm archipelago, Baltic Sea. *Estuarine Coastal and Shelf Science,* 61(2), pp. 339-349.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, pp. 487-515.

Finney, S., Pearce-Higgins, J. & Yalden, D. (2005). The effect of recreational disturbance on an upland breeding bird, the golden plover *Pluvialis apricaria*. *Biological Conservation,* 121(1), pp. 53-63.

Freestone, A.L. & Inouye, B.D. (2006). Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology,* 87(10), pp. 2425-2432.

Furness, R.W. & Camphuysen, C.J. (1997). Seabirds as monitors of the marine environment. *ICES Journal of Marine Science,* 54(4), pp. 726-737.

Gaston, K. & Spicer, J. (2004). *Biodiversity: an introduction. Second edition.* Blackwell Publishing, Oxford, UK.

Gaston, K.J., Jackson, S.E., Cantu-Salazar, L. & Cruz-Pinon, G. (2008). The ecological performance of protected areas. *Annual Review of Ecology Evolution and Systematics*. 39, pp. 93-113.

Greenwald, D.N. & Bradley, C. (2008). Assessing protection for imperiled species of Nevada, USA: are species slipping through the cracks of existing protections? *Biodiversity and Conservation,* 17(12), pp. 2951-2960.

Gärdenfors, U.e. (2010). Rödlistade arter i Sverige - The 2010 Red List of Swedish Species. *ArtDatabanken, SLU. Uppsala*.

Heinänen, S., Erola, J. & von Numers, M. (2012). High resolution species distribution models of two nesting water bird species: a study of transferability and predictive performance. *Landscape Ecology,* 27(4), pp. 545-555.

Heinänen, S., Rönkä, M. & von Numers, M. (2008). Modelling the occurrence and abundance of a colonial species, the arctic tern *Sterna paradisaea* in the archipelago of SW Finland. *Ecography,* 31(5), pp. 601-611.

Heinänen, S. & von Numers, M. (2009). Modelling species distribution in complex environments: an evaluation of predictive ability and reliability in five shorebird species. *Diversity and Distributions,* 15(2), pp. 266-279.

Hildén, O. (1965). Habitat selection in birds: a review. *Proceedings of Annales Zoologici Fennici*. 2(1), pp. 53-75.

Jerling, L. & Nordin, U. (2007). *Bland skötar, kobbar och kor: Stockholms skärgård - uppkomst och utveckling*. Forskningsrådet Formas, p. 300.

Kessler, M., Abrahamczyk, S., Bos, M., Buchori, D., Putra, D.D., Gradstein, S.R., Hohn, P., Kluge, J., Orend, F., Pitopang, R., Saleh, S., Schulze, C.H., Sporn, S.G., Steffan-Dewenter, I., Tjitrosoedirdjo, S. & Tscharntke, T. (2009). Alpha and beta diversity of plants and animals along a tropical land-use gradient. *Ecological Applications,* 19(8), pp. 2142-2156.

Kindström, M. & Aneer, G. (2007). What is happening to our shores. *BALANCE Interim Report no. 26, Copenhagen, Denmark*(26), pp. 1-28.

Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye, B.D., Harrison, S.P. & Myers, J.A. (2011). Disentangling the drivers of beta diversity along latitudinal and elevational gradients. *Science,* 333(6050), pp. 1755-1758.

Lantmäteriet. (2014). Produktbeskrivning: GSD-Fastighetskartan, vektor [Product description: GSD-Property Map, vector]. Version 6.15. *The Swedish Mapping, Cadastral and Land Registration Authority.* Gävle [in Swedish].

Laursen, K., Kahlert, J. & Frikke, J. (2005). Factors affecting escape distances of staging waterbirds. *Wildlife Biology,* 11(1), pp. 13-19.

Leseberg, A., Hockey, P.A.R. & Loewenthal, D. (2000). Human disturbance and the chick-rearing ability of African black oystercatchers (*Haematopus moquini*): a geographical perspective. *Biological Conservation,* 96(3), pp. 379-385.

Loreau, M. (2000). Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecology Letters,* 3(2), pp. 73-76.

Mac Nally, R., Fleishman, E., Bulluck, L.P. & Betrus, C.J. (2004). Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. *Journal of Biogeography,* 31(6), pp. 917-929.

Magurran, A.E. & McGill, B.J. (2011). *Biological diversity: frontiers in measurement and assessment*: Oxford University Press, New York.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature,* 405(6783), pp. 243-253.

Meager, J.J., Schlacher, T.A. & Nielsen, T. (2012). Humans alter habitat selection of birds on ocean-exposed sandy beaches. *Diversity and Distributions,* 18(3), pp. 294-306.

Nordström, M., Laine, J., Ahola, M. & Korpimäki, E. (2004). Reduced nest defence intensity and improved breeding success in terns as responses to removal of non-native American mink. *Behavioral Ecology and Sociobiology,* 55(5), pp. 454-460.

Ojaveer, H., Jaanus, A., MacKenzie, B.R., Martin, G., Olenin, S., Radziejewska, T., Telesh, I., Zettler, M.L. & Zaiko, A. (2010). Status of biodiversity in the Baltic Sea. *Plos One,* 5(9), e12467.

Olsson, L. (2000). Handledning för kustfågelinventerare i Stockholms län. Version 1.0. *Sveriges Ornitologiska Förening. Kustfågelgruppen.* [in Swedish].

Ottvall, R., Edenius, L., Elmberg, J., Engström, H., Green, M., Holmqvist, N., Lindström, Å., Pärt, T. & Tjernberg, M. (2009). Population trends for Swedish breeding birds. *Ornis Svecica,* 19(3), pp. 117-192.

Pap, K., Nagy, L., Balogh, C., László, G. & Liker, A. (2013). Environmental factors shaping the distribution of common wintering waterbirds in a lake ecosystem with developed shoreline. *Hydrobiologia,* 716(1), pp. 163-176.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science,* 344(6187), pp. 987.

Pettersson, J. (2005). Kustfågelinventeringen i Uppsala län 2002 och 2003. Länsstyrelsens meddelandeserie 2005:6. [in Swedish]

Raup, D.M. & Crick, R.E. (1979). Measurement of faunal similarity in paleontology. *Journal of Paleontology,* 53(5), pp. 1213-1227.

Reed, S.E., Hilty, J.A. & Theobald, D.M. (2014). Guidelines and Incentives for Conservation Development in Local Land-Use Regulations. *Conservation Biology,* 28(1), pp. 258-268.

Reif, J., Storch, D. & Simova, I. (2008). The effect of scale-dependent habitat gradients on the structure of bird assemblages in the Czech Republic. *Acta Ornithologica,* 43(2), pp. 197-206.

Rissman, A.R., Lozier, L., Comendant, T., Kareiva, P., Kiesecker, J.M., Shaw, M.R. & Merenlender, A.M. (2007). Conservation easements: Biodiversity protection and private use. *Conservation Biology,* 21(3), pp. 709-718.

Roos, S. & Amcoff, M. (2011). Fågelfaunans utveckling i Uppsala läns skärgård efter införandet av jakt på mink. Länsstyrelsens Meddelandeserie 2010. [in Swedish]

Rosenstock, S.S., Anderson, D.R., Giesen, K.M., Leukering, T. & Carter, M.F. (2002). Landbird counting techniques: Current practices and an alternative. *Auk,* 119(1), pp. 46-53.

Rönkä, M., Tolvanen, H., Lehikoinen, E., von Numers, M. & Rautkari, M. (2008). Breeding habitat preferences of 15 bird species on south-western Finnish archipelago coast: Applicability of digital spatial data archives to habitat assessment. *Biological Conservation,* 141(2), pp. 402-416.

Sabine, J.B., Meyers, J.M., Moore, C.T. & Schweitzer, S.H. (2008). Effects of human activity on behavior of breeding American Oystercatchers, Cumberland Island National Seashore, Georgia, USA. *Waterbirds,* 31(1), pp. 70-82.

Sandström, A., Eriksson, B.K., Karås, P., Isæus, M. & Schreiber, H. (2005). Boating and navigation activities influence the recruitment of fish in a Baltic Sea archipelago area. *Ambio,* 34(2), pp. 125-130.

Sandström, J., Bjelke, U., Carlberg, T. & Sundberg, S. (2015). Tillstånd och trender för arter och deras livsmiljöer – rödlistade arter i Sverige 2015. ArtDatabanken Rapporterar 17. ArtDatabanken, SLU. Uppsala.

Sarkar, S. & Margules, C. (2002). Operationalizing biodiversity for conservation planning. *Journal of Biosciences,* 27(4), pp. 299-308.

Severcan, Ç. & Yamaç, E. (2011). The effects of flock size and human presence on vigilance and feeding behavior in the Eurasian Coot (*Fulica atra* L.) during breeding season. *Acta Ethologica,* 14(1), pp. 51-56.

SFS. (2009). The Swedish Environmental Code. Ds 2000:61. Available from http://www.regeringen.se/sb/d/574/a/22847.

Sorace, A. (2002). High density of bird and pest species in urban habitats and the role of predator abundance. *Ornis Fennica,* 79(2), pp. 60-71.

Statistics Sweden. (2014). Sveriges Officiella Statistik. Statistiska Meddelanden. MI 41 SM 1401. Skyddad natur 31 december 2013 – Protected Nature 2013. [in Swedish]

Stockholm County Board. (2004). Strandexploatering i Stockholms län. Mälaren och Östersjön. Länsstyrelsen i Stockholms län, Rapport 2004:05 Stockholm [in Swedish with English summary]

Sundblad, G. & Bergström, U. (2014). Shoreline development and degradation of coastal fish reproduction habitats. *Ambio,* 43(8), pp. 1020-1028.

Suurkuukka, H., Meissner, K.K. & Muotka, T. (2012). Species turnover in lake littorals: spatial and temporal variation of benthic macroinvertebrate diversity and community composition. *Diversity and Distributions,* 18(9), pp. 931-941.

Svensson, S., Svensson, M. & Tjernberg, M. (1999). Svensk fågelatlas. [The Swedish Breeding Bird Atlas.] Vår Fågelvärld, suppl. 31. Stockholm. p. 552.

Swedish Transport Agency. (2010). Båtlivsundersökningen 2010 – en undersökning om svenska fritidsbåtar och hur de används. Sollentuna. [in Swedish].

Theobald, D.M., Miller, J.R. & Hobbs, N.T. (1997). Estimating the cumulative effects of development on wildlife habitat. *Landscape and Urban Planning,* 39(1), pp. 25-36.

Tjorve, K.M.C. & Underhill, L.G. (2008). Influence of disturbance and predation on breeding success of the African Black Oystercatcher, *Haematopus moquini*, on Robben Island, South Africa. *Waterbirds,* 31(1), pp. 83-96.

Traut, A.H. & Hostetler, M.E. (2004). Urban lakes and waterbirds: effects of shoreline development on avian distribution. *Landscape and Urban Planning,* 69(1), pp. 69-85.

Tuomisto, H. (2012). An updated consumer's guide to evenness and related indices. *Oikos,* 121(8), pp. 1203-1218.

UN. (1997). Urban and Rural Areas, 1950–2030. New York, United Nations.

Watson, J.E.M., Dudley, N., Segan, D.B. & Hockings, M. (2014). The performance and potential of protected areas. *Nature,* 515(7525), pp. 67-73.

Veech, J.A. & Crist, T.O. (2007). Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. *Global Ecology and Biogeography,* 16(5), pp. 650-656.

Wetlands International. (2012). Waterbird population estimates, Fifth edition. Summary report. Wetlands International, Wageningen, The Netherlands.

Velando, A. & Munilla, I. (2011). Disturbance to a foraging seabird by sea-based tourism: Implications for reserve management in marine protected areas. *Biological Conservation,* 144(3), pp. 1167-1174.

Vellend, M., Verheyen, K., Flinn, K.M., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, B.J., Bellemare, J., Honnay, O., Brunet, J., Wulf, M., Gerhardt, F. & Hermy, M. (2007). Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *Journal of Ecology,* 95(3), pp. 565-573.

Whittaker, R.H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs,* 30(3), pp. 280-338.

Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C. & Pressey, R. (1996). A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology,* 10(1), pp. 155-174.

von Numers, M. (1995). Distribution, numbers and ecological gradients of birds breeding on small islands in the Archipelago Sea, SW Finland. *Acta Zoologica Fennica*, 197, pp. 1-127.

Wood, E.M., Pidgeon, A.M., Radeloff, V.C., Helmers, D.P., Culbert, P.D., Keuler, N.S. & Flather, C.H. (2015). Long-term avian community response to housing development at the boundary of US protected areas: effect size increases with time. *Journal of Applied Ecology*, in press.

Ås, S., Bengtsson, J. & Ebenhard, T. (1997). Archipelagoes and theories of insularity. *Ecological Bulletins*, 46, pp. 88-116.

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