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# Conserving what, where and how? Cost-efficient measures to conserve biodiversity in Denmark

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ABSTRACT

Biodiversity conservation efforts in Europe have traditionally focused on farmland and open nature areas such as grasslands, heathlands and meadows, while little attention has been devoted to conservation actions in forest. Using detailed information on the geographical distribution of about 900 terrestrial species in Denmark we apply systematic conservation planning techniques to identify how to protect biodiversity at the lowest cost to society. The results suggest that conservation actions in forest should be given a higher priority. Thus, three to four times the number of forest species are protected per million € compared with species living in open land natural areas. Furthermore, a gap analysis finds the current designation of Natura 2000 and other protected areas is skewed toward open land natural areas, and insufficient to meet the conservation targets on forest species.

## 1. Introduction

The rapid degradation and conversion of natural landscapes is resulting in an unprecedented loss of biological diversity and ecosystem services (Schipper et al., 2008; Butchart et al., 2010). Internationally, more than 175 countries are mandated, as signatories to the United Nation's Convention on Biological Diversity, to prepare National Biodiversity Strategy and Action Plans. The EU has declared the intention to halt the decline of biodiversity before 2020 (European Commission, 2012).

There is a need to identify conservation strategies which optimally balance economic costs and ecological constraints. Different land uses hold different conservation costs and conservation opportunities. For years, the European political emphasis has been on how to regulate farmers for halting the biodiversity decline. One prominent example is the European Common Agricultural Policy which since the early 1990s has supported agri-environmental schemes and promoted conservation objectives (Davies, 2004). The national funding of biodiversity protection in Denmark reflects that forests have not reached the same attention in the policy arena. If forest habitats hold a large share of the valuable biodiversity, lack of conservation support for forest areas may lead to loss of biodiversity and efficiency in the conservation policies.

The aim of this study is to explore this policy issue identifying where and which conservation efforts are needed to cost-efficiently protect a sample of terrestrial species in Denmark. It is also investigated whether current Danish conservation efforts are cost-efficient by comparing them to the 'optimal' conservation efforts found in the analysis.

The study applies a systematic conservation planning (SCP) approach to identify the most cost-efficient combination of geographically distributed habitats to be protected in order to reach a given level of protection. SCP approaches can support the design of conservation priorities that are more effective than merely ad hoc approaches (Margules & Pressey, 2000). This is interesting to academia, but spatial conservation prioritizations also appear to be increasingly adopted by practitioners (Groves et al., 2002; Morrison, Loucks, Long, & Wikramanayake, 2009) and the number

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of real-world applications, to both terrestrial and marine systems, is steadily increasing (Moilanen, Wilson, & Possingham, 2009). Although the SCP approach is still developing to account for ecological, economic, social, and political uncertainty, it may allow conservation managers to move beyond ad hoc conservation planning and increase the transparency in decision making (Langford et al., 2011; Ban et al., 2013; Game, Kareiva, & Possingham, 2013). SCP studies commonly include information on conservation costs to address the cost-efficiency and feasibility of conservation strategies (Ando, Camm, Polasky, & Solow, 1998; Naidoo et al., 2006; Lewis, Plantinga, Nelson, & Polasky, 2011) and reveal the trade-offs between costs and provision of biodiversity services as well as other services. Still a challenge remains in managing the transition from planning to applying conservation actions, taking into account both costs and benefits of future and presently protected areas. A number of studies have applied SCP at the national and EU scale to evaluate the effectiveness of conservation areas such as, e.g., Natura 2000 (Maiorano, Falcucci, Garton, & Boitani, 2007; Araujo, Alagador, Cabeza, Nogues-Bravo, & Thuiller, 2011; Jantke, Schleupner, & Schneider, 2011). However, to our knowledge few country studies have analysed and discussed in which habitats (land uses) the conservation efforts are most cost-efficient.

The study adds to current literature by linking costs with conservation actions and estimating the cost-efficiency of conservation efforts in different habitats. Even though the analysis is limited to a national case, the results and discussions are highly relevant for ongoing discussions of conservation efforts within the EU and elsewhere. We use the most comprehensive data set available to estimate the minimum – and most cost-efficient – effort needed to conserve Danish terrestrial biodiversity. In a systematic approach based on the principles of spatial conservation prioritization (Moilanen et al., 2009), we integrate information on species distribution, species habitat preferences, and current land use, as well as possible conservation actions and the associated social costs. Furthermore, the current conservation effort is considered.

## 2. Methods and data

In the presented scenarios we selected the most cost-efficient conservation network (species coverage compared to economic cost) using the complementary species richness principle (Pressey, Humphries, Margules, Vane-Wright, & Williams, 1993). Hereby the marginal contribution of a given site to the overall species representation in the conservation network is taken into account.

### 2.1. Species data

We used distributional data for various species groups in Denmark compiled for the 633 10 × 10-km UTM grid cells covering the country. The data record the presence or absence of each of the species in each of the grid cells. The data set covers a total of 899 terrestrial and a few semi-aquatic species breeding in Denmark.[1] Earlier versions and subsets of this data set have been previously used for quantitative biodiversity analyses (Lund & Rahbek 2002; Strange, Rahbek, Jepsen, & Lund, 2006a; Larsen et al., 2008, 2009, 2012; Bladt, Strange, Abildtrup, Svenning, & Skov, 2009). The data represent the most complete species distribution data in Denmark. The dataset includes several insect groups, all breeding vertebrates and a few groups of vascular plants in DK. Unfortunately, national atlas data on the remaining vascular plants, were not available for this study. The collection of national data on other important taxonomic groups e.g., bryophytes, lichens, and fungi, is in progress but found too incomplete for the current analysis. In order to enable separate analysis of threatened species protection, we created a subset of 186 (of the total 899 species) threatened species categorized as ‘Critically Endangered’ (CR), ‘Endangered’ (EN) and ‘Vulnerable’ (VU) in the Danish Red Data Book (Wind & Pihl, 2004).

**Table 1**
Habitat types and habitat preferences of species in the analyses[a].

| Habitat type | Area (km$^2$) | All species (number) | | Threatened species (number) | |
|---|---|---|---|---|---|
| | | Total | Obligate species | Total | Obligate species |
| Forest | 5000 | 503 | 186 | 81 | 39 |
| Open-land natural area | 3900 | 650 | 272 | 139 | 95 |
| Farmland | 30,700 | 240 | 1 | 15 | 0 |
| Urban areas | 3100 | 177 | 6 | 17 | 1 |
| Total | 43,000 | 899 | 465 | 186 | 135 |

[a] The majority of the species are found in forest and/or open land natural areas (888 of all 899 species), while the remaining 11 species are found only in farmland and/or urban areas (1 only in farmland, 6 only in urban areas and the remaining 4 in both farmland and urban areas).

Each species was associated with each of four general habitat types (forest, open land natural areas, farmland and urban areas) according to the habitat(s) in which they are most commonly found. Open land natural areas are defined as all non-forested habitats like grassland, heathland, meadows, bogs, salt marches, and sand dunes. This also includes semi-natural grasslands, while farmland is defined as intensively cultivated areas with associated small scale habitats only. The information on habitat preference was based on expert assessments compiled specifically for this study or taken from the Danish Red Data Book (Wind & Pihl, 2004). The data are summarized in Table 1.

A distinction is made between obligate species, which are found in only one of the four habitat types, and non-obligate species, which are found in more than one habitat type. Because of the large number of obligate species (458) in forest and open land, the minimum network required to cover these was identified in a preliminary analyses. It turned out that this network also “automatically” covers most of the non-obligate species and species found in farmland and/or urban areas. This means that no or only marginal gains (in terms of cost-efficiency) can be obtained by including farmland or urban areas in a general species conservation strategy in Denmark. Therefore, the analyses presented below focus only on forest and open land natural areas—and the 888 species found in these two habitats. The 11 species that are found only in farmland and/or urban areas are excluded and should be handled in a separate strategy.

Even though the data set includes large numbers of both forest and open land natural area species (Table 1) the data may be somewhat skewed toward open land natural area species. Table 2 shows that 72% of our 899 species are found in open land nature as compared to 54% of 8008 species assessed in the Danish Red Data Book, which is a much larger sample of the Danish species pool, estimated at 35,000–40,000 species (excluding microorganisms). However, this is expected to have a minor effect on the overall results since the two habitats are analysed separately.

The predominance of open habitat species in our data is also reflected in the species richness across the country, as illustrated

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[1] These are 5 reptile species, 13 amphibians, 181 birds, 48 mammals, 41 dragonflies (Odonata), 23 grasshoppers (Orthoptera), 60 true bugs (Heteroptera: Pentatomidea, Coreoidea, Pyrrhocoridea), 21 click beetles (Coleoptera: Elateridae), 248 hoverflies (Diptera: Syrphidae), 58 butterflies (Lepidoptera: Hesperioidea, Papilionoidea), 154 large moths (Lepidoptera: Hepialoidea, Cossoidea, Zygaenoidea, Tineoidea, Yponomentoidea, Bombycoidea, Geometroidea, Sphingoidea, Notodontoidea, Noctuoidea), 6 club mosses (Lycopodiaceae) and 35 orchids. The data include the majority of the Danish species within each group except for the click beetles, which mainly include species associated with old forest. We excluded vagrant, casual and exotic species from the data set to avoid bias toward those species.

**Table 2**
Distribution of species among habitat preferences in the data set applied in the present analysis compared to data from the Danish Red Data Book (compilation based on Wind and Pihl, 2004).

| | Proportion of all species (*N*) found in forest | | Proportion of all species (*N*) found in open land natural areas | |
|---|---|---|---|---|
| | Total | Obligate | Total | Obligate |
| Present data set (*N* = 899) | 56% | 21% | 72% | 30% |
| DK Red Data Book (*N* = 8008) | 64% | 36% | 54% | 23% |

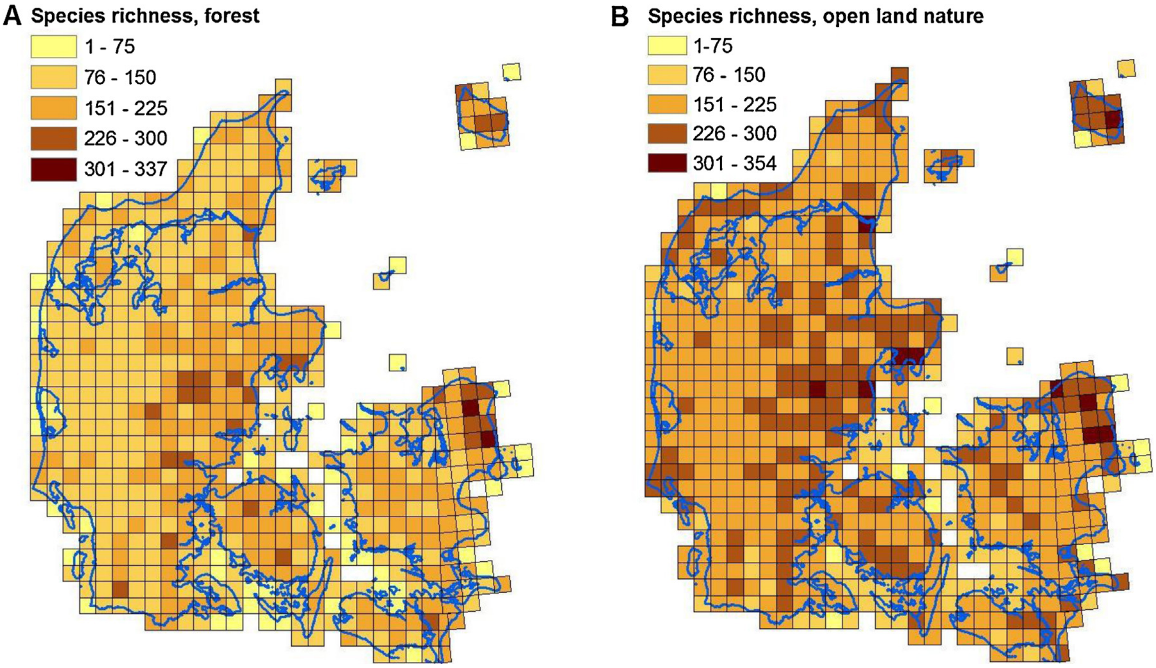

**Fig. 1.** Distribution of the species richness in Danmark in forest (A) and open land nature (B). Map based on 899 species included in the present analysis. Intensively cultivated farmland is not included in the analysis.

in Fig. 1, but the overall spatial patterns in forest and open land natural areas appear quite similar.

### 2.2. Habitat and Natura 2000 data

The national distribution of the four general habitat types is based on available land cover and land use maps. The 2006 version of CORINE land cover map (European Environment Agency, 2007; Stjernholm, 2009) was used as starting point. However, the minimum mapping unit size of 25 ha excludes many smaller areas. In order to construct a more complete map, two additional data sources are applied: (1) The land use map from the national "Area Information System" (Danish Ministry of Environment, 2000) and (2) the official registration of heathland, grassland, bogs, meadows, and salt marches in accordance with Section 3 in the Danish Nature Protection Act. Forest and open land natural areas were compiled as the sum of relevant habitats in all sources. The remaining land area was classified as farmland or urban areas. Lakes above 0.25 ha were excluded, but smaller lakes were retained as natural parts of the surrounding habitats. Based on the final GIS-map, the area of each habitat in each of the 633 grid cells was calculated.

To compare the resulting cost-efficient networks of areas with areas currently protected, GIS-maps of Danish Natura 2000 sites and other protected areas (according to national regulations) were obtained from the Danish Ministry of Environment (www.miljoeportal.dk). The Natura 2000 sites include Special Protected Areas (EC Birds Directive 1976) and Sites of Community Interest (EC Habitats Directive 1992).

### 2.3. Conservation actions and their cost

A number of specific threats and potential mitigating conservation actions were identified from national sources (The Danish Board of Technology, 2008; Ejrnæs et al., 2011; Rahbek et al., 2012) and from discussions with Danish conservation experts. Subsequently, the experts assessed which conservation actions would significantly improve of the survival probabilities of local populations of threatened species within the next couple of decades.

The chosen conservation actions in forest include an immediate stop of forest intervention and drainage in broadleaved forests, allowing for conversion of commercial production forests into unmanaged forests with natural hydrology. Unmanaged forests will increase the continuity of the forest cover and gradually increase the amount of dead wood, as well as variation and dynamics with respect to tree species, age structure and density. Additionally, smaller adjacent areas of coniferous plantation forest are harvested to provide open areas within the forest, in order to further increase the habitat diversity. These areas are subsequently left for natural succession and, if needed, future maintenance to prevent the invasion by shrubs and trees.

The actions in open land natural areas comprise three components: (1) Maintenance of existing natural areas, (2) increased area (expanding the current natural areas), and (3) reduction of nutri-

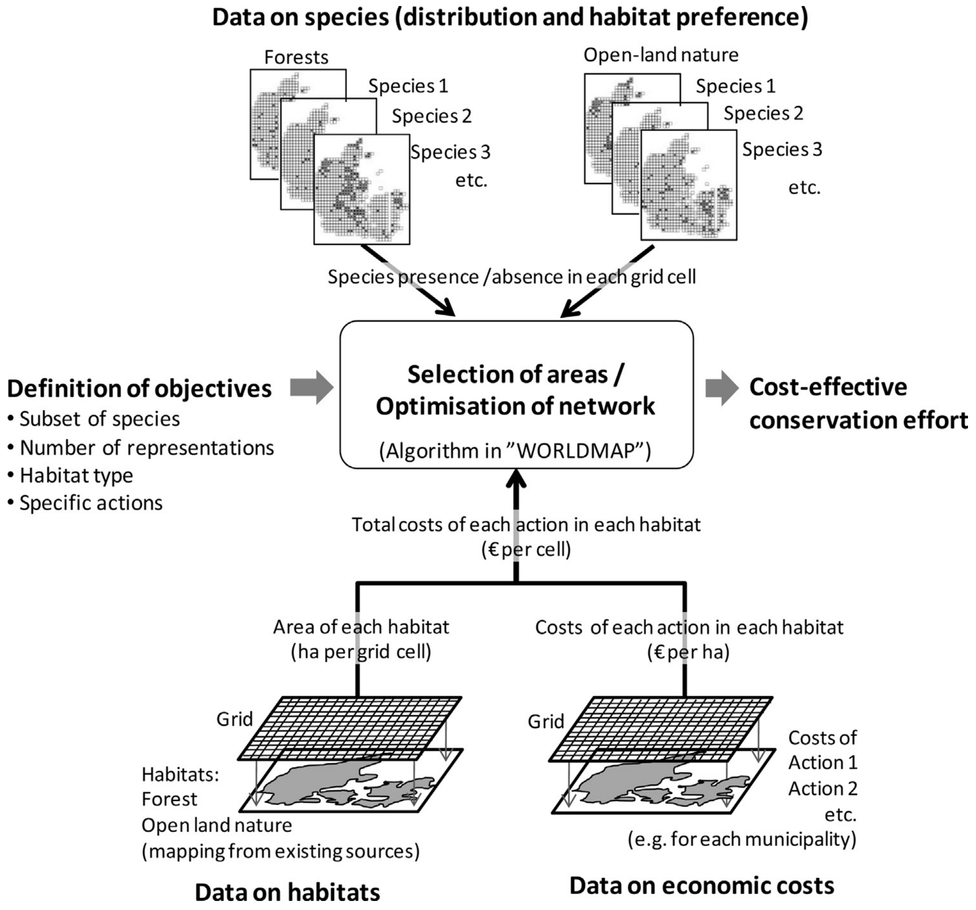

**Fig. 2.** Applied data and principles of the analysis. Data on species distribution in forest and open land natural areas are used to select areas (grid cells) for conservation networks based on the principle of complementarity. Areas are selected in order to minimize the total cost (social cost) as calculated from the area specific cost of selected conservation actions and the distribution (area) of the habitats.

ent pollution. Maintenance includes grazing, harvest of hay and/or clearing of scrub, to prevent invasion by shrubs and trees. Open land natural areas in Denmark are typically very fragmented, and increasing the area is believed to benefit the survival of species through increased ability to maintain viable (meta) populations. The third action includes 250 m buffer zones around each open land natural area, in which livestock production facilities should no longer be permitted. This action reduces the deposition of airborne nitrogen pollutants (ammonia), which is recognized as one of the major general threats to the biodiversity in open land nature in Denmark (Ejrnæs et al., 2011).

As a general rule the actions must be implemented in the entire area of the relevant habitat in the selected cells. However, conservation of 3000 ha of each habitat in each cell (=30% of a 10 × 10 km cell) was established as the realistic maximum effort in each cell (gap requirement sensu De Klerk, Fjeldså, Blyth, & Burgess (2004)), allowing for other land uses at a local level. The proposed conservation actions are summarised in Table 3. Note that the conservation actions are assumed to be essential in order to preserve the biodiversity within the sites. The choice and effect of the included conservation actions are further discussed in Section 5.

The social cost of each of the conservation actions has been calculated as the annual cost in 2010-price level (measured in consumer prices). The social cost consists of opportunity costs and direct costs. The opportunity cost is loss of production value of alternative use of the different areas, i.e., loss of agricultural or forest production. The direct costs are the cost of labor and other inputs used for carrying out maintenance activities on current and new open land natural areas and cleared forest areas. Estimates of the direct costs are based on Hasler and Schou (2004), Dubgaard et al. (2012), and Hasler et al. (2012), who find only small variation in maintenance cost across the country and various types of open habitats. Therefore, we apply one average maintenance cost. As the existing open land natural areas must remain in their current land use we estimate the conservation cost in these areas as merely the maintenance cost. The maintenance of existing open land natural areas is subsidized by the EU. In new areas the maintenance measures are the same but the actual cost is higher since they are not subsidized by the EU (Table 3).

The opportunity costs of lost forest production is based on spatial data on tree species, tree age and site classes used in biometric models and finally combined with forecasts of prices of wood products. The cost of forest production is calculated at municipality level as regional differences in costs of conservation actions should be taken into account when determining the optimal geographical allocation of land conservation. The cost ranges are shown in Table 3.

The costs of increasing open land natural areas are calculated as the price of farmland, which reflects market's expectations for future earnings of the agricultural production.[2] We use land price at municipality level, which reflects geographical variations in, e.g.,

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[2] The price of farmland also includes the value of future subsidies to farmland from EU. Normally loss of a subsidy should not be considered a social cost (only a transfer of money from one party to another). However, from a narrow Danish point of view the loss of a subsidy from EU can be regarded as a social cost. The subsidy to farmland paid by the Danish state is deducted from the farmland price.

**Table 3**
Conservation action and their social cost.

| Action | Description | Area | Area specific costs | |
|---|---|---|---|---|
| | | | Calculation | € per ha per year |
| Forest | | | | |
| Conversion to ”natural” unmanaged forest | Forestry abandoned in broadleaved forest | All broadleaved forest in each cell is converted | Opportunity costs of abandoning forestry in broadleaved forest[a] | 70–330 € |
| | Supplementary cut down of coniferous forest in adjacent areas | If available, coniferous forest is cut down in an area corresponding to 20% of the broadleaved forest | Opportunity costs of abandoning forestry in coniferous forest[a] | 30–250 € |
| | And subsequent maintenance | | Maintenance of open areas | 240 € |
| Open land natural areas | | | | |
| Maintenance of existing areas | Existing open land habitats are maintained typically through grazing, harvest of hay and clearing of scrub | All open land natural areas in each cell up to a maximum of 3000 ha | Ongoing costs of typical maintenance methods One overall average of different methods and habitats | 140 € |
| Increased area | The area of open land habitats is increased by including adjacent farmland | If farmland is available the area is doubled—except that the resulting area should not exceed 3000 ha in one cell | Opportunity costs of abandoning cultivated areas[a] | 620–940 € |
| | The additional area is maintained | | Maintenance costs as described above | 240 € |
| Reduction of ammonia pollution | Buffer zones around open land natural areas are established in which no livestock production facilities are allowed | 250 m buffer zones around existing natural areas if farmland is available | Costs of abandoning livestock production facilities within the buffer zones recalculated into cost per ha (of the open land natural areas) | 150 € |

[a] For these actions regional variation was derived from municipality based cost estimates. For the remaining actions uniform costs were applied nationwide.

soil quality. Finally, the cost of ammonia buffer zones is calculated as the cost of reducing the capacity of stables and farm buildings within the buffer zone, subject to the assumption that these buildings have limited value for other uses. The different opportunity costs are all measured as a “one-time loss”. To calculate the annualized value of this loss we use an annual real rate of return of 3%.

### *2.4. Scenarios and analyses*

Four scenarios are analysed. In all scenarios the same analytical conservation objective was applied: each species must be represented in at least three grid cells—or in their full distribution range, if this is only one or two cells. Each species can be represented in forests and/or open land natural areas, depending on their habitat preferences. We use multiple species representations since the focus of the SCP design is on the national persistence. Compared to just one representation, the applied minimum requirement reduces the risk of species extinction, since species are maintained within the reserve network, even if local extinctions occur (Cabeza & Moilanen, 2001). As will be shown, most of the species in the cost-efficient conservation network are represented more than three times. The selection of areas is based on the economic costs of the conservation actions described above. As described in Section 2.1, we focus on selecting forest areas and open land natural areas, ignoring farmland and urban areas.

In the first scenario (A) we include all the 888 species found in forest and or open land natural areas. In the second scenario (B) we only include the subset of 184 threatened species. In these two scenarios we identify the minimum effort needed to preserve the species without considering any previous or planned conservation efforts.

In order to compare the results of scenarios A and B with the current conservation policies we make the assumption in scenarios C and D that habitats inside existing conservation areas are already protected. Given this assumption we calculate the minimum additional conservation network outside existing protected areas needed to fulfill the conservation objectives used in previous scenarios. These analyses are carried out for all nature conservations areas in Denmark (scenario C) and for Natura 2000 areas alone (scenario D). The last scenario is included because of the strong focus on the Natura 2000 obligations in the present Danish nature management and the general European perspective. Similar gap analyses have been used by, e.g., De Klerk et al. (2004) and Strange, Rahbek, Jepsen, and Lund (2006b). The different scenarios are summarized in Table 4.

### *2.5. Overview of data and optimization procedure*

For the optimization process and selection of conservation networks we use the heuristic progressive rarity algorithms of the WORLDMAP software, including a specific procedure to include cost parameters (Margules, Nicholls, & Pressey, 1988; Williams, 1998; Williams et al., 2003). Such simple algorithms have been demonstrated to give a close approximation to the mathematically optimal solution (Csuti et al., 1997; Moore et al., 2003). In each specific analysis we identify the near-minimum set (Williams, 1998) cf. the minimum set coverage approach (Pressey et al., 1993). The data and the optimization framework are summarized in Fig. 2. For each species we use information on its national spatial distribution as presence/absence in 633 10 × 10 km grid cells combined with information on its habitat preference (upper part of Fig. 2). We also include data on the area of each habitat type per grid cell combined with the estimated area specific cost of the conservation actions required in these habitats (lower part of Fig. 2). In each analysis we identify the conservation network which minimizes the social

**Table 4**
Overview of scenarios.

| Scenario | A | B | C | D |
|---|---|---|---|---|
| Species included | All (888) | Threatened (184) | All (888) | All (888) |
| Restriction on selection of areas | No restriction | No restriction | Needed area outside Natura 2000 (gap-analysis) | Needed area outside protected areas (gap-analysis) |
| Species representation[a] | 3 | 3 | 3 | 3 |

[a] Minimum three geographic representations when possible (some species are only found in 1 or 2 grid cells).

costs of a given analytical objective. Each objective is defined by the subset of species, the minimum species representation and the required conservation actions. In the gap analyses (Scenarios C and D), priority is given to existing protected areas by setting the conservation cost in these to zero. In this way we maximise the effort (area) inside the protected areas (within the scope of the conservation objective) and simultaneously calculate the additional effort outside the areas needed to meet the conservation objective.

## 3. Results

The minimum cost conservation network from scenario A includes areas in 172 grid cells distributed throughout Denmark (Fig. 3). In most of these cells conservation actions should be implemented either in forests or in open land natural area, while in 23 grid cells both habitats are targeted.

Core results for this conservation network are shown in Table 5. The total area of the network is 125,000 ha before the enlargement of the open land natural areas. After the enlargement the total area of the network becomes 167,000 ha, which corresponds to 4% of the total Danish land area. The total social cost of the suggested conservation actions is estimated at € 94.9 million per year. The network includes more grid cells selected for conservation in open land natural areas than in forest areas. In accordance with this, open land natural areas constitute 62% of the total network area. The difference in terms of costs is even more pronounced as 87% of the total costs are allocated to open land natural areas, reflecting the higher area specific costs in open land natural areas. The number of species covered in the open land natural areas is also higher. However, a comparison of the number of protected species in the two habitats with the conservation costs reveals that three to four times the number of species are protected per million € in the forest compared with open land nature (Table 4). It is important to note that these estimates only illustrate the relative difference between the habitats. They cannot be interpreted as the absolute price per species conserved because only a small subset of all the terrestrial species is included in the analysis. In practice far more than these 888 species would be protected in the conservation network. Still, the results strongly suggest that it is cost-efficient to give forest a high conservation priority. This conclusion is strengthened by the fact that a large proportion of all Danish species, probably the majority, is found in the forest (cf. Table 2).

The conservation areas and costs are described in more details in Table 6. It appears that the conservation network includes about 20% of the total area of broadleaved forests and open land natural areas in Denmark. It also appears that in the open land natural areas different conservation actions all contribute substantially to the total conservation costs. In accordance with these, the selected areas should be increased by 42,000 ha, reaching a total of 120,000 ha of protected open land natural areas in scenario A. The additional area for the 250 m ammonium buffer zones around these areas corresponds to 7% of current farmland area in Denmark.

The chosen conservation objective was that all species should be represented in at least three different grid cells in the selected network except for species that are found in only one or two cells. In scenario A, 64 species are protected across their entire distribution range of one, two or three grid cells (Fig. 4). Another 32 species are represented in exactly three grid cells, even though they have larger range sizes (i.e., present in more grid cells). However, the majority of species are protected in more locations and almost two thirds are protected in more than 20 different grid cells. These are typically rather common and non-threatened species.

The selection of areas in the network is to a large extent determined by the rare species in terms of range size. This is illustrated by the red grid cells in Fig. 5, which host species that are only found in 1–3 grid cells. These cells are irreplaceable as they must be included in the network in order to fulfill the conservation objective. In con-

**Table 5**
Minimum cost conservation network for all 888 species found in forest and/or open land natural areas (scenario A).

| | Forest | Open land nature | Total |
|---|---|---|---|
| Number of grid cells | 86 | 109 | 172[d] |
| Initial size of selected areas (1000 ha)[a] | 47 | 78 | 125 |
| Annual cost of conservation actions (million €) | 12.2 | 82.7 | 94.9 |
| Number of obligate species protected[b] | 238 | 385 | 458 |
| Total number of species protected[c] | 473[c] | 608[c] | 888 |
| Obligate species/annual costs (*N*/million €) | 19.5 | 4.7 | 4.8 |
| All species/annual costs (*N*/million €) | 38.8 | 7.4 | 9.4 |

[a] For open land habitats one of the conservation actions is to increase the size of the natural area. The table shows the size before the enlargement.

[b] Obligate species here means species found either in forest or in open land natural areas (not in both), ignoring the fact that some of them are also found in farmland and/or urban areas.

[c] Total number of obligate or non-obligate species represented in at least three grid cells in each habitat (or in their full range size if this is only one or two cells). As 215 non-obligate species meet this criterion in both habitats, the sum of species in the two columns is larger than 888. For 22 species representation in both habitats is needed to fulfill the criterion.

[d] In 23 of these grid cells both forest and open land natural areas are selected cf. Fig. 3.

**Table 6**
Break-down of conservation costs in the mimimum cost conservation network for all 888 species (scenario A).

| Conservation actions | Annual costs (million €) | Area(ha) | Proportion of national area |
|---|---|---|---|
| Forest | | | |
| Unmanaged broadleaved (forestry ban) | 9 | 39,000 | 21% of broadleaved forest |
| Cut down of coniferous | 2 | 8000 | 2% of coniferous forest |
| Maintenance of cut down areas | 2 | | |
| Open land nature | | | |
| Maintenance of existing areas | 12 | 78,000 | 20% of open land natural areas |
| New areas from farmland | 30 | 42,000 | 1% of farmland area |
| Maintenance of new areas | 10 | | |
| Ammonium buffer zones | 30 | 194,000 | 7% of farmland area |
| Total | 95 | 361,000 | |

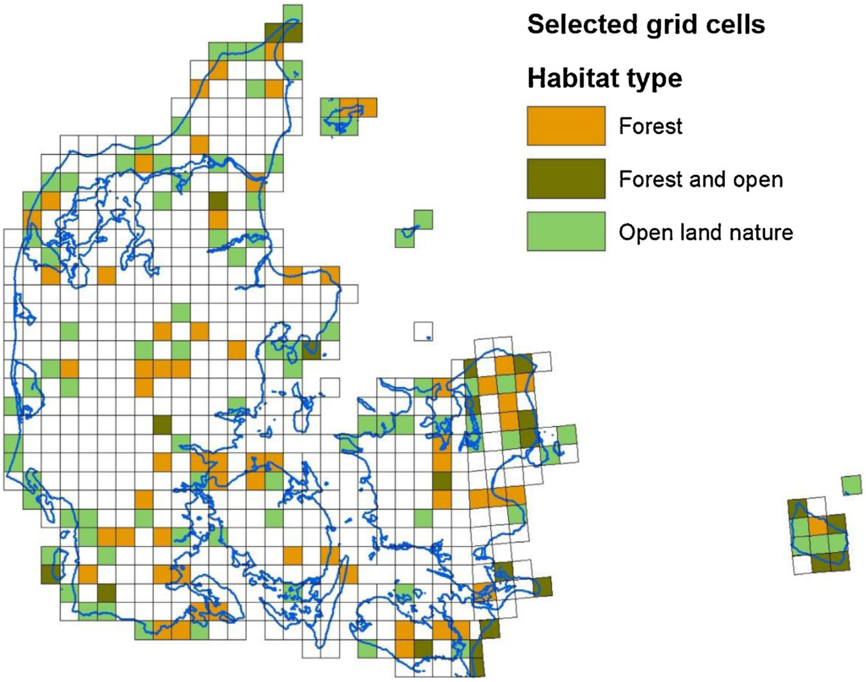

**Fig. 3.** Locations of forest and open nature in the minimum cost conservation network for all 888 species (scenario A).

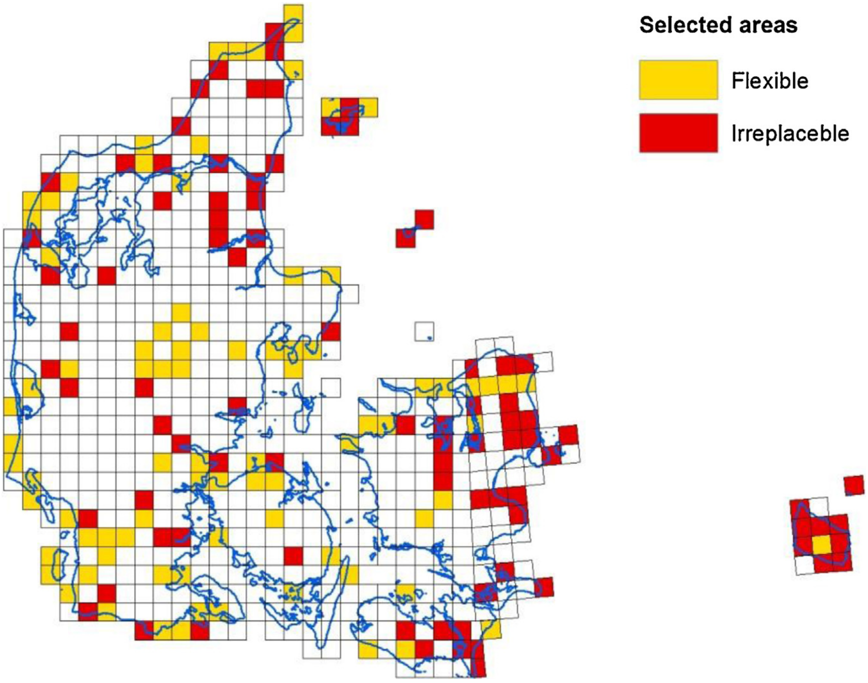

**Fig. 5.** Flexibility in the minimum cost conservation network for all 888 species (Scenario A). Yellow grid cells are (partly) flexible. They could be replaced by other grid cells, but at a higher social cost. Red cells are irreplaceable with respect to at least one habitat type (forest or open land nature). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

trast, the yellow grid cells can be replaced by one or more other cells, though at a higher overall social cost.

As the majority of the grid cells are irreplaceable, the results suggest that there is little flexibility in the choice of areas given the objective of protecting all species in at least three different locations. It implies that the species distribution rather than the costs of conservation actions determines which areas to include in the conservation network. The lack of flexibility also has implications for the choice of policy instruments. We will return to this in the discussion.

If a conservation network is selected focusing only on the 184 threatened species (scenario B), the, number of grid cells and the total area needed to meet the conservation goal are lower than in scenario A as are the social cost. However, the reduction is fairly modest (Table 7). Thus, the annual social costs of protecting the 184 threatened species are € 81.3 million, which corresponds to 86% of the costs of the conservation network for all 888 species.

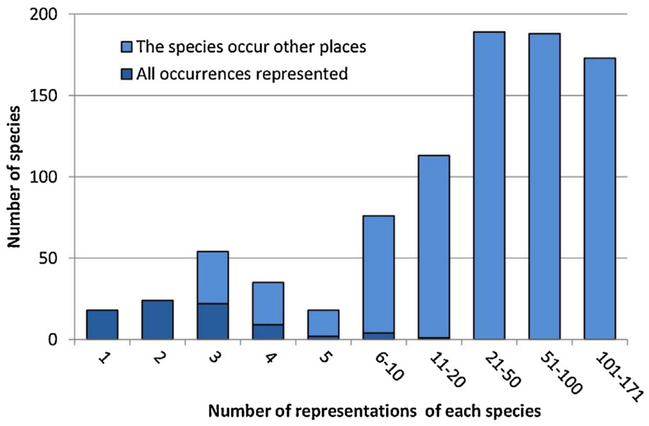

**Fig. 4.** Representation of species in the minimum cost conservation network for all 888 species (scenario A).

**Table 7**
Minimum cost conservation network for the 184 threatened species (scenario B).

| | Forest | Open land nature | Total |
|---|---|---|---|
| Number of grid cells | 65 | 93 | 138[d] |
| Initial size of selected areas (1000 ha)[a] | 38 | 70 | 108 |
| Annual cost of conservation actions (million €) | 10.3 | 71.0 | 81.3 |
| Number of obligate species protected[b] | 45 | 103 | 148 |
| Total number of species protected[c] | 63[c] | 120[c] | 184 |
| Obligate species/annual costs (*N*/million €) | 4.4 | 1.5 | 1.8 |
| All species/annual costs (*N*/million €) | 6.1 | 1.7 | 2.3 |

[a] For open land habitats one of the conservation actions is to increase the size of the natural area. The table shows the size before the enlargement.

[b] Obligate species here means species found either in forest or in open land natural areas (not in both), ignoring the fact that some of them are also found in farmland and/or urban areas.

[c] Total number of obligate or non-obligate species represented in at least three grid cells in each habitat (or in their full range size if this is only one or two cells). As 10 non-obligate species meet the criterion in both habitats and 11 species must be represented in both habitats to fulfill the criterion, the sum of species in the two columns does not correspond to the total of 184 species.

[d] In 21 of these grid cells both forest and open land natural areas are selected cf. Fig.3.

### 3.1. *Comparing with existing conservation areas in Denmark*

In order to investigate the extent to which our 888 species are covered by existing conservation areas, we conducted gap analyses (Scenarios C and D) to calculate the additional conservation network outside existing reserves needed to fulfill the same conservation objective as in Scenario A.

The total land area in Denmark subject to some kind of nature protection amounts to 544,000 ha. This is more than three times the area (167,000 ha), which according to our analysis is needed for making a cost-efficient conservation network covering all species in our data set (Scenario A). In accordance with this, the gap analysis (Table 8) shows that for (existing) open land natural area, the conservation goal can be met almost entirely within existing reserves (97% of the required area). In contrast, only 51% of the required forest area can be found in existing reserves, while additional 24.000 ha must be selected outside.

It is important to note that the protected areas included in the gap-analysis represents several categories, some of which are not subject to very strong protection levels. Thus, the Danish Nature Protection Act does not enforce the maintenance of all protected areas outside Natura 2000. Generally, the present Danish nature conservation policy has a strong focus on Natura 2000 sites. They cover an area of about 358,000 ha, which is still more than two times the area needed for a cost-efficient conservation network in our analysis. Nevertheless, the gap analysis (Scenario D), shows that a substantial effort is needed outside the Natura 2000 network (Table 8) both in forest and open land natural areas. About 58,000 ha of existing natural areas outside Natura 2000 has to be protected in order to reach the conservation target. This means that only about half of the required conservation network is currently covered by the Danish Natura 2000 sites, even without considering the suggested enlargement of open land natural areas. Again, there is a substantial difference between forest and open land nature, as only 44% of the required forest area is part of the Natura 2000 network, while this is the case for 63% of the required (existing) open land area.

## 4. Discussion

The aim of our study was to estimate the extent and costs of the effort needed to conserve Danish terrestrial biodiversity. We have accomplished that by identifying a cost-efficient conservation network protecting almost 900 species through relevant conservation actions in the main natural habitats. The analysis indicates that 167,000 ha of natural areas are required at a cost of 95 € million per year. This corresponds to 4% of the Danish land area and 0.04% of the Danish Gross Domestic Product. An effort of this magnitude will most likely cover the majority of the 35–40,000 terrestrial species living in Denmark. This assumption is supported by the general predominance of medium to large range species in Denmark indicated by the data, which suggests that most of the remaining species will be found in the resulting large complementary based conservation network. Furthermore, rare and more specialized species may tend to aggregate in the same (rather few) high quality natural areas in Denmark (Strange et al., 2006a; Larsen et al., 2008).

We have applied the best species distribution data currently available. Nevertheless, the possible future addition of further taxonomic groups might change the priority of habitats and specific areas and reveal the need for additional areas in order to fulfill the conservation objectives. Furthermore, some conservation actions not considered in our analysis may be needed to preserve particular species including the obligate farmland and/or urban species, which were excluded from our analyses. The results should thus be regarded as lower bound estimates of the required national conservation efforts and costs. On the other hand the analyses disregards if some of the conservation actions are already implemented.

Halting the loss of biodiversity is a political goal both in Denmark and globally. Identifying cost-efficient conservation schemes is thus important regardless of the benefits of preserving biodiversity. Nevertheless a comparison of the observed conservation costs with the potential benefits is relevant. The benefits of preserving generally well-functioning ecosystems may be immense. The more specific benefits are very hard to estimate, but an increasing number of environmental valuation studies on biodiversity shows that the Danish public is willing to offer substantial economic support to the protection of biodiversity. The annual willingness to pay per household is estimated at € 1–2 per threatened species, when correcting for hypothetical bias in the stated preference study, and marginally decreasing with the number of protected species (Jacobsen, Boiesen, Thorsen, & Strange, 2008). The average willingness to pay for terrestrial habitat and biodiversity protection is approximately € 100 per house hold per year, amounting to a national estimate of € 250 million per year in Denmark (Jacobsen, Lundhede, & Thorsen, 2011). Comparing the societal benefits with the estimated cost of approximately € 100 million per year suggests that conservation pays off from a socio-economic point of view.

We find that large gains in protection effectiveness and cost-efficiency can be expected from allocating conservation effort to protect valuable forest habitats compared to open land natural

**Table 8**
Gap analysis in relation to existing nature conservation areas in Denmark. Additional area needed to cover all 888 species in forest and or open land nature if the effort inside protected areas is maximized[a]. Upper panel: all conservation areas. Lower panel: natura 2000 sites alone.

| Habitat | Maximized effort inside protected areas | | Additional effort outside protected areas | | Total | |
|---|---|---|---|---|---|---|
| | Area (1000 ha) | % of total | Area (1000 ha) | % of total | Area (1000 ha) | % of total |
| All protected areas | | | | | | |
| Forest | 25 | 51% | 24 | 49% | 50 | 100% |
| Open land | 80 | 97% | 2.7 | 3.4% | 83 | 100% |
| Total | 105 | 80% | 27 | 20% | 132 | 100% |
| Natura 2000 sites | | | | | | |
| Forest | 22 | 44% | 28 | 56% | 50 | 100% |
| Open land | 51 | 63% | 30 | 37% | 81 | 100% |
| Total | 73 | 56% | 58 | 44% | 131 | 100% |

[a] Note that the area of the network from the gap analysis does not include the enlargement of open land natural areas.

areas and buffer zones in agricultural areas. This contrasts to the current Danish nature policy as illustrated by our gap-analyses and the fact that economic support to conservation initiatives in open land natural areas is significantly higher than initiatives in the forests. Approximately € 140 million was allocated from the EU Rural Development Programme for nature protection in 2012, but less than 5% of this funding is spent on protected forest areas (Danish Economic Councils, 2012). This Programme mainly aims at protecting biodiversity in farmland including semi-natural open land habitats, while financial support for biodiversity conservation in forests largely remain a national issue requiring public financing and funding from private foundations. Our analyses indicate that even the designation of Natura 2000 areas in Denmark is biased toward non-forested habitats. It could be argued that the Natura 2000 scheme focusses on habitats of European interest and is not intended to provide a representative range of sites for conservation at a Member State level. However, the Danish national forest inventory has revealed many locations outside the Danish Natura 2000 network with forest habitat types listed in the EU-Habitats Directive (Johannsen, Nord-Larsen, Riis-Nielsen, Suadicani, & Jørgensen, 2013); and the share of such areas seems to be higher than for open land habitat (Ejrnæs,Moeslund, & Bladt, 2014). Our finding is supported by Ejrnæs et al. (2014) who used high resolution presence data to demonstrate that the number of redlisted species in Danish forests is higher outside than inside the Natura 2000. They argue that the relevant habitats outside the Natura 2000 areas tend to be small and fragmented, which may have disqualified many areas in the designation process. The protection of forest biodiversity may also have been given low political priority for historical and cultural reasons. Even intensively managed forests in Denmark are often perceived by the general public as "natural areas" less influenced by humans than cultivated agricultural areas. Furthermore, habitats like grasslands, heathlands and meadows are often perceived by the general public as threatened and under pressure from intensive agriculture, urban development and invasion by shrubs while this is not the case for forest per se, since the forest area actually has increased in the last two centuries.

The findings should stimulate a debate on the possible mismatch between actual priorities and alternative strategies involving larger conservation gains. The observed bias toward non-forested habitats in Denmark cannot be justified by the EU biodiversity conservation policies or by the global Convention on Biological Diversity. On the other hand, the funding of agri-environmental schemes under the EU Rural Development Programme may have contributed to the bias since similar economic support has not been available for forest conservation. This is problematic as it may constitute a general issue within the EU Member countries, which reduces both the effectiveness and cost-efficiency of current national and EU conservation policies. This analysis illustrates the possible gains from a better integration of policies.

The objective in Scenario A was to protect all species in the data set irrespective of red list status. This approach is assumed to reduce the risk that presently non-threatened species will become threatened in the future. We also demonstrate that this strategy is only about 20% more costly than the alternative strategy focusing only on the threatened species (Scenario B). However, since the network based on threatened species also hosts most of the non-threatened species (Petersen, Strange, Anthon, Bjørner, & Rahbek, 2012), the true marginal cost for each remaining non-threatened species is larger.

Appropriate estimates of conservation cost are crucial for the development of efficient protection strategies (Frazee, Cowling, Pressey, Turpie, & Lindenberg, 2003; Naidoo et al., 2006). We combine opportunity costs and maintenance costs and provide a more realistic estimate of the implementation cost compared with earlier attempts (Ando et al., 1998; James, Gaston, & Balmford, 2001, However, we largely exclude other implementation costs such as transaction and negotiation costs (Naidoo et al., 2006) and social data relevant for the implementation success (Knight, Cowling, & Campbell, 2006, Knight, Cowling, Difford, & Campbell, 2010). Implementation of large-scale conservation actions may affect conservation costs. A number of studies have demonstrated that conservation actions may affect the availability of land, resulting in increasing land prices and potential acquisition costs. We ignore the dynamic effects of such changes in supply and demand, even though we expect they would most likely increase the pricing of land and conservation costs (Phelps, Carrasco, Webb, Koh, & Pascual, 2013).

The present analyses are based on only a few conservation actions chosen to target forest and open land natural areas defined very broadly. Natural questions would be whether these actions will actually work and why a broader array of actions is needed in open land nature as compared to the forest? This is important, since the different actions contribute very much to the estimated difference in cost-efficiency between the two habitats. First of all, the proposed actions were chosen to mitigate important general threats in the relevant habitats. Commercial forestry in Denmark has for almost two centuries been very intensive, making use of even aged monocultures, removal of understory vegetation and dead wood, clearcuttings, soil treatment and pesticides as well as extensive draining. This practice poses a threat to forest biodiversity because it inevitably interrupts forest continuity and reduces or eliminates an array of natural habitats. Reduced forest intervention will benefit a large range of species including saproxylic insects and hole-dwelling birds as well as epiphytes and fungi (Friedel, von Oheimb, Dengler, & Härdtle, 2006; Ódor et al., 2006; Brunet, Fritz, & Richnau, 2010; Müller & Bütler 2010; Lassauce, Paillet, Jactel, & Bouget, 2011; Müller et al., 2013). The supplementary clearings of coniferous stands adjacent to and within the unmanaged broadleaved areas is assumed provide open spaces and mixed habitats that will benefit other species like vascular plants and insects dependent on light, temperature or nectar resources (Gittings, O'Halloran, Kelly, & Giller, 2006; Naaf & Wulf 2007; Liivamägi, Kuusemets, Kaart, Luig, & Diaz-Forero, 2014). Accordingly, the proposed change of commercially managed production forest into more natural unmanaged forest will certainly improve the persistence of forest biodiversity in the long term.

In Denmark and other northern temperate areas, most of the large natural grazers are extinct. In such regions maintenance to prevent the invasion by shrubs and trees is most often needed for preserving non-forested open land nature and the associated biodiversity. Even though the lack of grazers will also affect forest habitats, much of the forest biodiversity will thrive under more unmanaged conditions. This is why we include maintenance costs for only a minor part of the selected forest area.

The habitat size requirement varies between species. However, at the general level larger areas of a certain habitat are likely to host larger and more viable populations than smaller areas, and for species displaying meta-population dynamics increased area can turn smaller sink populations into larger source populations (Hanski & Gilpin, 1991; Hanski, 1999). Therefore, we assume the suggested enlargement of the area of open land natural areas will promote species persistence (Rouget, Cowling, Lombard, Knight, & Kerley, 2006). Similarly, the proposed conversion of production forest into unmanaged forest will increase the area and connectivity of critical forest habitats and thus the persistence of populations.

Finally, actions to reduce airborne nutrient pollution was only considered in open land, because such pollution poses a serious threat to biodiversity particularly in nutrient poor open habitats (The Danish Board of Technology, 2008; Ejrnæs et al., 2011; Rahbek et al., 2012).

Some further assumptions of our analyses should be considered. As we downscale the area selection from entire grid cells to the area of relevant habitats, we assume that the species actually are present in those habitats. Given the predominance of intensive farmland and urban areas in the remaining land, we believe this assumption is met in most cases. Another issue is the lack of direct evidence that the selected species occurrences represent long-term viable populations. However, it has been shown that for larger areas (like Denmark) species occurrence is a good surrogate variable for persistence, i.e., for viable populations (Araújo, Williams, & Fuller, 2002, Araújo, Williams, & Turner, 2002). Furthermore, the analysis assumes that actions are implemented, which will increase the probability of species survival. The analyses only distinguish between forest and non-forested (open land) habitats, which may be seen as an oversimplification. However, for our purpose this is sufficient and, very importantly, it is simple. A further division of species on habitats would most likely involve more subjective and uncertain assessments. Even if we distinguish between different open land habitats this would have minor impacts on the overall allocation results, since Hasler and Schou (2004), Dubgaard et al. (2012), and Hasler et al. (2012) found little variation in maintenance cost across habitat types.

Three representations of each species may be considered a low minimum requirement, which in the long run may invoke a significant risk of national extinction. On the other hand, three representations ensure that extinction of single populations due to stochastic events will not automatically lead to national extinction. Furthermore, it may leave some flexibility if societal needs would require an alternative prioritization of conservation areas. Finally, as a result of the near-minimum analysis approach most species are much better protected. In scenario A, 92% of all species are represented five times or more. A larger minimum requirement could be more effective in maintaining species over time, but it would also be more costly. Running the analysis with a minimum requirement of five representations shows that approximately 50% more area is needed to fulfill this objective. Hence, the costs are expected to grow proportionally with the size of the minimum representation, although it will level off at a certain level.

The current conservation planning analysis has focused on the spatial allocation of conservation actions without considering the policies or incentives needed to achieve the right actions in the right areas. In the last decades voluntary and flexible economic instruments have been advocated to promote biodiversity. As an example of voluntary economic instruments, the OECD (2010) recommended the use of auctions where landowners submit payment bids on how much they need to be compensated for undertaking a given biodiversity conservation action on their land.

Economic instruments like auctions are primarily advantageous when the flexibility is high; implying that several areas mutually replaceable without compromising the target and to some extent the cost. The present analysis based on Danish data indicates, however, only little flexibility in the choice of areas. A large fraction of the areas must be protected in order to meet the target, because they host species with range sizes of three cells or less (Fig. 5). For these areas it is hardly beneficial to use auctions. Basically, the landowners in question may display monopolistic behavior when bidding, if the government has announced its intention to preserve all species.

Spatial conservation prioritization techniques have advanced rapidly since the 1980s (Pressey, Whish, Barrett, & Watts, 2002; Moilanen et al., 2009), addressing an increasingly complex and realistic suite of conservation contexts (Wilson, Carwardine, & Possingham, 2009). However, the application of these techniques has been criticized that they remain largely theoretical (Prendergast, Quinn, & Lawton, 1999; Whitten, Holmes, & MacKinnon, 2001; Knight, Driver et al., 2006). The preliminary results of this study have been discussed with stakeholders from the agricultural and forestry sectors, the World Wildlife Foundation and other environmental non-governmental organizations, and members of the Danish Parliament at national workshops. This topic appeared to be highly controversial. The forestry sector has disputed that forests should be a more important habitat for protection of biodiversity than farmland and open land natural areas. When confronting the forestry sector with the logical steps and assumptions behind the analysis they oppose against it as they fear it will lead to the close down of the forestry sector in Denmark. In terms of economic size and political power the Danish forestry sector is much less important than the agricultural sector. However, our analysis also shows that an increased effort in the forests is not enough. The majority of the conservation investments still need to be allocated to agriculture to protect species in semi-natural habitats or to abandon cultivated areas. Interestingly, a number of Danish political parties referred to our findings in their recent general election campaigns. This illustrates that such structured decision analysis may play an important role in framing the challenges political decision makers are facing for the future protection of biodiversity in an extensively managed landscape such as the Danish.

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