Gap analysis of European wetland species:
priority regions for expanding the Natura 2000 network

Kerstin Jantke[a,b], Christine Schleupner[a], and Uwe Andreas Schneider[a,c]

[a] Research Unit Sustainability and Global Change, University of Hamburg, KlimaCampus Hamburg, Bundesstrasse 55, 20146 Hamburg, Germany
[b] International Max Planck Research School on Earth System Modelling,
Max Planck Institute for Meteorology, Bundesstrasse 53, 20146 Hamburg, Germany
[c] International Institute for Applied Systems Analysis, Schlossplatz 1, 2361 Laxenburg, Austria

Corresponding author:
Kerstin Jantke
Research Unit Sustainability and Global Change
KlimaCampus, University of Hamburg
Bundesstrasse 55, 20146 Hamburg, Germany
telephone +49 40 428387090, fax +49 40 428387009
kerstin.jantke@zmaw.de

Published in *Biodiversity and Conservation*

The final publication is available at www.springerlink.com

http://dx.doi.org/10.1007/s10531-010-9968-9

Abstract

Protected areas in the European Union under the Natura 2000 reserve system cover about 17 percent of the total land area. Systematic evaluations of the effectiveness of the current reserve system have been scarce and restricted to regional assessments. One reason for that may be the poor availability of comprehensive fine scale biodiversity data for the highly fragmented and densely human-populated European continent. We apply recently developed modeling tools for systematic conservation planning to conduct a detailed gap analysis using coarse scale species occurrence data. The employed mathematical model uses mixed integer programming to determine the cost-minimizing distribution of habitat locations subject to biophysical, economic, and policy restrictions. We include fine scale wetland habitat data as well as species-specific proxies for population density and viable population threshold. First, we evaluate the performance of the current Natura 2000 system in covering endangered wetland vertebrate species. Results show that five area-demanding vertebrates are not covered by the current reserve system. Second, we identify potentials for expanding the network to move toward complete coverage for the considered species mostly in countries of North-Eastern Europe. About 3 million hectares of additional reserve area at a cost of 107 million Euro per year would be required to achieve coverage of all considered species. Third, we present spatially explicit priority regions for a cost-effective expansion of the current reserve network.

Key words: effectiveness of reserve systems, mathematical programming model, persistence, representation, population viability, systematic conservation planning

Introduction

Protected areas are the foundation for most national conservation policies. Accordingly, governments around the world have made commitments to establish systems of protected areas that conserve viable representations of terrestrial, freshwater, and marine ecosystems (IUCN 2003). 12.9 % of the global terrestrial area is formally protected although only 5.8 % is within strictly protected areas (IUCN categories I-IV) (Jenkins and Joppa 2009). However, little is known of the extent to which these areas contribute to the goal of protecting biodiversity (Brooks et al. 2004; Rodrigues et al. 2004a). Many systems of protected areas are not representative of national biodiversity, as their selection is rather biased towards economically marginal landscapes (Pressey et al. 2002; Rouget et al. 2003; Scott et al. 2001).

Europe is one of the world's most densely human-populated continents and has a long and complex cultural history. The cornerstone of the nature and biodiversity policy in the European Union is Natura 2000. This European Union-wide network of protected areas is regulated mainly by two directives: the 1979 Birds Directive and the 1992 Habitats Directive. The Natura 2000 network consists of Special Protection Areas and Sites of Community Importance whose objectives are to assure the long-term maintenance of Europe's endangered species and habitats at "favorable conservation status" (European Commission 2009a). Without doubt, Natura 2000 is the most important initiative for biodiversity conservation in Europe (Gaston et al. 2008; Pullin et al. 2009). Weber and Christopherson (2002) call Natura 2000 the most ambitious supranational initiative for conservation that has ever been undertaken.

About 17 % of the European Union's land area is currently designated as protected under Natura 2000 (European Commission 2009b). Despite these efforts, Europe has not achieved the target of halting the loss of biodiversity by the end of 2010 (European Environment Agency 2009; Butchart et al. 2010). The vast majority of the European continent's terrestrial area is still subject to extensive habitat degradation and limited protection (Hoekstra et al. 2005). The sufficiency index of the European Commission reveals considerable shortfalls in the progress of member states in designating protected areas (European Environment Agency 2009). Meanwhile, 40-85 % of habitats and 40-70 % of species of European conservation concern have reached an unfavorable conservation status (European Environment Agency 2009). This trend also includes progressive declines in wetlands across Europe during the last decades (Jones and Hughes 1993). The effectiveness of the Natura 2000 network in maintaining biodiversity has been assessed in few studies and incompletely (Rondinini and Pressey 2007; Maiorano et al. 2007; Gaston et al. 2008). Previous studies are limited to regional assessments. For example, a study by Dimitrakipoulos et al. (2004) shows that the Natura 2000 sites on the Greek island Crete represent regional plant biodiversity insufficiently. Araujo et al. (2007) and Maiorano et al. (2007) find that the Natura 2000 network contributes notably to biodiversity protection in two European Union regions, Italy and the Iberian Peninsula. Nevertheless, both studies conclude that the network needs to be strengthened and complemented by further protected areas. To our knowledge, the entire spatial entity of the European Union with the complete species and habitats assemblage of the Natura 2000 related directives has so far not been assessed for completeness.

Systematic conservation planning provides tools to identify priority areas for conservation. It can be defined as a structured, target-driven approach accounting for two basic principles of any system of protected areas: (i) representativeness, the need to capture the full variety of biodiversity at all levels of organization; and (ii) persistence, the long-term survival of species and ecosystems (Margules and Pressey 2000; Margules and Sarkar 2007). Persistence can be further subdivided into the concepts of resiliency and redundancy (Shaffer and Stein 2000). Both principles are essential for the long-term survival of a species or ecosystem. According to Shaffer and Stein (2000), the size of sites on which a species or ecosystem occurs may be seen as a measure of resiliency, and the number of sites as a measure of redundancy. Gap analysis is the part of systematic conservation planning which evaluates the performance of existing reserve systems. This approach has a long history and is applied e.g. in the Gap Analysis Program (GAP) in the U.S. (Scott et al. 1993), focusing on the comprehensiveness of existing protected area networks and the identification of gaps in coverage. After the review of actual reserves, the need for additional areas to achieve specific conservation targets is addressed. Therefore, priority areas for expansion of existing reserve systems are identified in a subsequent planning stage. Both elements, reviewing existing reserves and identifying additional priority areas, are of importance in a meaningful conservation planning assessment. Numerous gap analyses at global (Rodrigues et al. 2004a, b; Jenkins and Joppa 2009) and regional scales (Fearnside and Ferraz 1995; Ramesh et al. 1997; Powell et al. 2000; Scott et al. 2001; Dietz and Czech 2005; O'Dea et al. 2006; Ceballos 2007; Catullo et al. 2008; Nel et al. 2009; Pinto and Grelle 2009) reveal that coverage of species and ecosystems by existing networks of protected areas is insufficient for the long-term maintenance of biodiversity. The issue of gap analysis has reached attention in Europe only recently. European forests are the focus of a gap analysis by Smith and Gillett (2000). Oldfield et al. (2004) show that most types of natural areas are underrepresented in England's reserve system. Two studies by Maiorano et al. (2006, 2007) address terrestrial vertebrates in the Italian protected areas. Araujo et al. (2007) find that the reserve system on the Iberian Peninsula needs to be enlarged to adequately cover terrestrial plant and vertebrate species.

To evaluate the current status of biodiversity and to determine how conservation efforts can be improved, biodiversity monitoring is crucial (Balmford et al. 2005). However, the poor availability of fine scale biodiversity data hinders scientifically sound conservation planning in Europe (Gaston et al. 2008). While species distribution data have been better mapped in Europe than in most other regions worldwide, there is a considerable difference between the spatial resolution of biodiversity data and the relatively high resolution of fragmented habitat data (Araujo 2004; Gaston et al. 2008). Gaston et al. (2008) argue that species atlas data are too coarse for most conservation planning exercises. The resulting planning units from coarse species occurrence data are too large to serve as planning units in these assessments. A study on reserve sizes in England (Oldfield et al. 2004) finds that most protected areas are far smaller than the resolution of biodiversity data, making it difficult to know whether species recorded in a particular planning unit actually occur inside corresponding protected areas. Nonetheless, several studies use European biodiversity data despite their coarse resolution. Priority areas for complementing reserve systems in Spain are identified with species atlas data of 50 km resolution (Benayas and de la Montana 2003). A study by Araujo et al. (2007) employs similar data to evaluate the effectiveness of Iberian protected areas in the conservation of terrestrial biodiversity.

We agree with Margules and Pressey (2000) and Maiorano et al. (2006) that conservation planning should not be delayed until improved biodiversity data are available. Conservation planning questions may be asked at different scales of thematic and spatial resolution. Hence, also coarse-scale assessments can provide important insights in how to shape conservation strategies. As biodiversity losses can be irreversible, delayed conservation actions may leave fewer options for the future. Here, we conduct a detailed gap analysis using coarse scale species occurrence data. Being aware of the limitations of our approach due to the data deficiencies, we discuss the possible implications on a potential widening of the Natura 2000 reserve system. In view of the dramatic decline in wetlands across Europe during the last decades (Jones and Hughes 1993; European Commission 2007) and several recent studies highlighting notable gaps in protected area systems for freshwater ecosystems (Yip et al. 2004; Abellán et al. 2007; Sowa et al. 2007; Nel et al. 2009), our study focuses on freshwater wetland species and their habitats. Our analysis covers the European Union. Specifically, the aims of our study are: (1) to assess the performance of the existing Natura 2000 network in covering threatened vertebrate wetland species and their habitats with respect to representation and persistence, (2) to identify potentials for expanding the network cost-effectively, (3) to derive explicit maps delineating wetlands promising for an expansion of Natura 2000.

Methods

We perform a gap analysis in four stages (Fig. 1). We (I) develop conservation targets to guide the assessment; (II) compile data on the planning region; (III) assess the performance of the current system of protected areas; and (IV) identify priority regions for expanding the system. These steps are similar to those proposed by Margules and Pressey (2000) for a systematic conservation planning assessment.

Figure 1 about here

Conservation targets

According to our conservation target approach, a species is considered as covered by the existing reserve system, when (i) representation and (ii) persistence criterions are met simultaneously. A species is (i) represented once when at least one occurrence is recorded inside Natura 2000 sites. We assume the (ii) persistence criterion to be fulfilled when two conditions are met. First, each representation corresponds to at least one viable population of that species. A population is considered viable when the allocated land area meets the minimum critical area, which is a species-specific measure based on density data and minimum viable population sizes. Second, the land area that corresponds to the minimum critical area of a species is allocated to habitat types required by that species. The concept of minimum critical area has been applied in similar gap analyses of mammal species in Florida (Allen et al. 2001) and of primates in the Atlantic forest reserve system of Brazil (Pinto and Grelle 2009). To account for redundancy and enable more than one representation of a viable population, the conservation target is stepwise increased in the model application.

Data

Study area and existing Natura 2000 network

Our study area comprises the European Union with 26 out of 27 member states. We exclude Cyprus and the Portuguese and Spanish islands in the Atlantic Ocean due to data deficiencies. The European Union covers a terrestrial area of 4,303,351 km² of which approximately 40 % is cultivated, while 4 % are urban areas (European Commission 2010). About 500 million people inhabit the region (European Commission 2010), resulting in a population density of 116 inhabitants per km². The landscape is highly fragmented (Hoekstra et al. 2005).

About 17 % of the European Union’s land area is protected under the Natura 2000 framework. Until November 2009, 22,419 Sites of Community Importance with a total area of approximately 717,000 km² and 5,242 Special Protection Areas with a total area of approximately 575,000 km² have been submitted to the European Union for approval. For Sites of Community Importance, the national territory covered ranges from 6.8 % in the United Kingdom to 31.4 % in Slovenia. For Special Protection Areas, the percentage of national territory covered ranges from 2.9 % in Ireland to 25.1 % in Slovakia. About 90 % of the reserves are smaller than 1,000 ha (European Commission 2009b). The spatial data on the Natura 2000 sites have been provided by the European Commission, DG Environment (2008) (data on Austria and United Kingdom) and the European Environment Agency (2010) (updated data on other European Union countries).

Target species

We include 70 vertebrate wetland species listed in the appendices of the Birds and Habitats directive which encompass 16 amphibians, 4 reptiles, 41 breeding birds, and 9 mammals. Occurrence records were obtained from Gasc et al. (1997), Hagemeijer and Blair (1997), and Mitchell-Jones et al. (1999). The terrestrial parts of all 2237 grid cells of 50 km resolution (UTM projection) encompassing the European Union serve as planning units.

Species-specific minimum critical areas are calculated from density data and minimum viable population sizes. Species’ density data are derived from a literature review; we use the maximum observed density. Proxies for minimum viable population sizes are based on Verboom et al. (2001). Data on habitat type requirements are taken from the literature as well. We distinguish five wetland habitat types including peatlands, wet forests, wet grassland, water courses, and water bodies. Furthermore, the type “open water” is applied to species that require either water courses or water bodies. We also distinguish required and optional habitat types. To enable the most area-demanding species to fulfill their area requirements, they are allowed to inhabit a certain share of non-wetland habitat. See Appendix A for the ecological data included for the 70 species.

Distribution of wetland habitats

Similar to the poor availability of fine scale species distribution data, spatial data on the distribution of European wetlands are either incomprehensive or they are of coarse resolution and illustrating wetland areas of large extent only (Schleupner 2010a). To consider wetland habitats adequately in our analysis, we estimate high resolution data on existing functional wetlands and suitable wetland restoration areas with the Spatial Wetland Distribution model (SWEDI; Schleupner 2010b). This empirical model comprises the most recent and comprehensive database on European freshwater wetland distribution. The Spatial Wetland Distribution model distinguishes three main wetland types including peatlands, wet forests, and wet grasslands, at 1 km² resolution. Out of it wetland areas are calculated for each planning unit of the HABITAT model. Spatial data on extent and distribution of open waters are extracted from the Coordination of information on the environment (CORINE) land cover data (European Environment Agency 2000) and the Global Lakes and Wetlands Database (Lehner and Döll 2004). To put the current status of wetland protection in perspective, we differentiate three types within and outside Natura 2000 sites: a) recent existing wetland areas by wetland type, b) potential restoration areas by wetland type, c) open waters (sub-divided into water courses and water bodies). Table 1 shows the areas of the above categories summed over the whole study region. Due to scaling, uncertainties, and other deficiencies, these areas should only be considered as estimates rather than accurate observations.

Table 1 about here

Land cost data

Designating additional protected areas involves costs. These costs may include acquisition costs, management costs, transaction costs, and opportunity costs (Naidoo et al. 2006). Here, we address the acquisition and opportunity costs of land. These two cost types will usually equal if there is no market revenue from land after conservation and if there are no externalities involved in the alternative use (Bladt et al. 2009). Country-specific data on current agricultural land rents are taken from European land statistics from Eurostat (http://epp.eurostat.ec.europa.eu/) and Farm Accountancy Data Network (http://ec.europa.eu/agriculture/rica/index_en.cfm) (see Appendix B for the detailed data and sources).

The HABITAT model

Planning units

HABITAT is a deterministic, spatially explicit model with planning units of varying shape and size. There are two possible states of each planning unit; it is either used as a species' reserve (1) or not (0). Status (1) is requires that a species has been historically observed in a planning unit. Selecting a planning unit for conservation does not necessarily allocate the entire planning unit's reserve area. Only those fractions of planning units are chosen which are necessary to fulfill the respective conservation target for all species. In case a species' minimum critical area or habitat type requirement cannot be fulfilled within a single planning unit, the model selects further habitat in adjacent planning units. For a detailed description see also Jantke and Schneider (2010).

Mathematical model structure

This section documents the mathematical formulation of the HABITAT model. The equation syntax includes specific symbols for sets, endogenous variables, and exogenous data.

Sets:

- $c = \{1,\ldots,C\}$ is the set of countries
- $p = \{1,\ldots,P\}$ is the set of planning units
- $t = \{1,\ldots,T\}$ is the set of habitat types

- $q = \{1,\ldots,Q\}$ is the set of habitat qualities
- $s = \{1,\ldots,S\}$ is the set of species.

We employ several set mappings, which contain possible combinations between two or more individual sets. In particular,

- $u(s,t)$ identifies the mapping between species and habitat types and
- $k(s,p,t)$ the possible existence of species and habitats in each planning unit.

Variables:

- N denotes the total number of conservation targets achieved by the included species. This variable is important for the first part of the gap analysis; the assessment of current protection levels of the Natura 2000 network.
- O represents total opportunity costs summed across all regions. This variable is necessary for the second part of the gap analysis; the identification of priority regions for expanding the network.
- Z_c represents the opportunity cost in country c.
- $Y_{p,t,q}$ depicts the protected habitat area for planning unit p, habitat type t, and habitat quality q in hectares.
- $X_{p,s}$ denotes a binary variable array with $X_{p,s} = 1$ indicating that planning unit p fulfils the habitat requirements for one viable population of species s, and $X_{p,s} = 0$ otherwise.

All variables except the objective variables N and O are restricted to nonnegative values.

Exogenous data:

- $r_{c,p}$ depicts the annual land rent per hectare in country c and planning unit p
- $a_{p,t,q}$ contains the maximum available area for planning unit p, habitat type t and habitat quality q
- $d_{s,q}$ represents species- and habitat quality-specific population density data
- m_s is a species-specific proxy for the minimum viable population size
- $h_{t,s}$ determines non-substitutable habitat requirements for habitat type t and species s
- t_s is the representation target for species s

- v_s specifies possible deviations and equals the difference between the general representation target and exogenously calculated occurrence maxima.

$$\text{Maximize} \qquad N = \sum_{p,s} X_{p,s} \qquad [1a]$$

$$\text{Minimize} \qquad O = \sum_{c} Z_c \qquad [1b]$$

subject to:

$$Z_c = \sum_{p \in c,t,q} Y_{p,t,q} \cdot r_{c,p} \qquad \text{for all c} \qquad [2]$$

$$Y_{p,t,q} \leq a_{p,t,q} \qquad \text{for all p,t,q} \qquad [3]$$

$$\sum_{p} X_{p,s} \geq t_s - v_s \qquad \text{for all s} \qquad [4]$$

$$\sum_{q} Y_{p,t,q} \geq h_{t,s} \cdot X_{p,s} \qquad \text{for all p,t,s} \qquad [5]$$

$$\sum_{t,q} d_{s,q} \cdot Y_{p,t,q}\Big|_{k(s,p,t) \wedge u(s,t)} \geq m_s \cdot X_{p,s} \qquad \text{for all p,s} \qquad [6]$$

$$\sum_{p,t,q} d_{s,q} \cdot Y_{p,t,q}\Big|_{k(s,p,t)} \geq t_s \cdot m_s \qquad \text{for all s.} \qquad [7]$$

The first objective function [1a] maximizes viable occurrences of species across all species and planning units. The second objective function [1b] minimizes total costs across all planning units. Note that in each simulation only one of these two objectives is active. Equation [2] calculates the total conservation costs in each country as product of habitat area times land price summed over all planning units. Constraint [3] limits habitat areas in each planning unit to given endowments. Constraint [4] implements representation targets for all species but allows deviations if the number of planning units with occurrence data is below the representation target. Constraint [5] depicts minimum requirements of non-substitutable habitat types for relevant species and planning units. Constraint [6] forces the habitat area for the conservation of a particular species to be large enough to support viable populations of that species. The summation over habitat types depicts the choice between possible habitat alternatives. Constraint [7] ensures that the total population size equals at least the representation target times the minimum viable population size. This constraint is especially relevant for cases where the representation target is higher than the number of available planning units for conservation. For example, a representation target of ten viable populations with possible species occurrences in only nine planning units would under [7] require one or more planning units to establish enough habitat for more than one viable population. The problem is programmed in General Algebraic Modeling System (GAMS) and solved with a mixed integer programming algorithm from CPLEX version 12.1.

Assessment of current wetland biodiversity protection

The first part of this assessment estimates how much biodiversity is currently protected within the Natura 2000 network. In the HABITAT model, we activate objective equation [1a] to maximize the number of distinct viable occurrences of species within the sites of the existing Natura 2000 network. The extent and habitat composition of the Natura 2000 sites are captured by the parameter $a_{p,t,q}$ which depicts the maximum available area for planning unit p, habitat type t and habitat quality q. To ensure that each species is covered at least once, the representation parameter t_s is set to 1.

We apply three possible states depicting the coverage of a species inside a reserve system. We define a species as (i) fully covered if all recorded occurrences lie within protected areas and the corresponding habitat size equals for every occurrence at least the minimum critical area for that species. If a species with several recorded occurrences fulfils the conservation target at least once, we consider it as (ii) covered, and otherwise to be a (iii) gap species. Given the coarse occurrence data, we need to assure that the species regarded as fully covered or covered by the HABITAT model are actually present in the protected areas of the Natura 2000 network. Therefore, we validate the model results with the species lists of the Natura 2000 viewer (http://natura2000.eea.europa.eu/) and the EUNIS biodiversity database (http://eunis.eea.europa.eu/).

Identification of priority regions for expanding the Natura 2000 network

As the existing Natura 2000 system does not fulfill the ambitious targets of national and international conservation objectives mentioned earlier, additional areas may be required to reduce or resolve the particular shortfalls. We address such demands in the second part of this assessment and determine the cost-minimizing locations of additional protected areas promising to expand the reserve system. In the model, we activate objective equation [1b] to minimize the total opportunity costs for a potential widening of the existing Natura 2000 network. The extent and habitat composition of the total unsealed land area inside and outside the Natura 2000 sites are depicted by the parameter $a_{p,t,q}$. We set the lower bounds of the variable array $Y_{p,t,q}$ to the extent and habitat composition of the Natura 2000 sites. One viable representation of a species in a reserve system, by definition, depicts only the absolute minimum to preserve this species over time within a relatively constant environment. Because of ecological and anthropogenic disturbances such as extreme weather events, epidemics, climate change, or certain economic activities, the minimum value will hardly guarantee long time survival. The representation parameter t_s is therefore stepwise increased from 1 to 10 to force redundancy of species' viable populations in an enhanced Natura 2000 system.

Delineation of potential sites for expansion

The identified priority regions for expanding the Natura 2000 network are downscaled with the Spatial Wetland Optimization Modeling Project (SWOMP; Schleupner 2009). The Spatial Wetland Optimization Modeling Project is based on spatial analyses using ArcGIS 9.2 as well as the analysis tools V-late and Hawths Analysis Tools (2006; Lang and Tiede 2003; Tiede 2005). Through the ArcGIS Model Builder function and Python Scripting, the downscaling process is automated. In the model, the restoration variables are computed iteratively until the maximum wetland area defined by the expansion area per planning units and wetland type is reached. Figure 2 summarizes the model structure.

Figure 2 about here

The Spatial Wetland Optimization Modeling Project gives preference to the protection of existing functional wetlands over restoration of degraded and conversion of other potential sites. The assessment of the most suitable sites relies on spatial criteria including enlargement (protected wetland sites might be enlarged by adjacent unprotected wetlands), connectivity (to build regional biotope complexes, evaluated by the proximity index after Gustafson and Parker (1992)), wetland size (determination of the desired minimum or maximum size of a wetland), and range (wetlands within a certain distance to other restored/existing wetlands or conservation areas of importance). The relative weight of individual criteria depends on the conservation objectives.

The determination of suitable wetland expansion sites also depends on their economic suitability. This suitability is based on three parameters including land value (opportunity costs of land to be converted into wetland), conversion cost (restoration success and costs valued after potential natural vegetation and land use), and neighborhood value (areas prioritized after area quality by using the hemeroby concept). The spatial-ecological criteria described above can be used optionally in addition to these three parameters to determine the most qualified sites within the allocated economic adequate areas. The result is a map showing the most promising sites for an expansion of the Natura 2000 network. For a detailed description of the Spatial Wetland Optimization Modeling Project see Schleupner (2009).

Results

Performance of current Natura 2000 network in covering wetland species

The first part of our gap analysis shows that only two species are (i) fully covered in the existing Natura 2000 system. All recorded occurrences of the Dutch root vole (*Microtus oeconomus arenicola*) and the Pannonian root vole (*Microtus oeconomus mehelyi*) lie within protected areas with their area requirements for viable populations fulfilled. Furthermore, we consider 61 other species as (ii) covered. According to our model, 21 species of this set are represented by hundred or more populations. We identify seven species as (iii) gap species, namely the spotted eagle (*Aquila clanga*), the golden eagle (*Aquila chrysaetos*), the black stork (*Ciconia nigra*), the osprey (*Pandion haliaetus*), the European otter (*Lutra lutra*), the Corsican painted frog (*Discoglossus montalentii*), and the Mallorcan midwife toad (*Alytes muletensis*). These seven species are represented inside several Natura 2000 sites, but their minimum area and/or habitat requirements are not met.

The validation of these results with the Natura 2000 viewer and the EUNIS biodiversity database revealed two discrepancies. First, although recorded as covered in our analysis, there are no recent records of the Lesser White-fronted Goose (*Anser erythropus*) within Natura 2000 sites in its breeding range. The Fennoscandian population of Lesser White-fronted Goose has declined rapidly since the middle of the 20th century and is facing an immediate risk of extinction (Jones et al. 2008; Tolvanen et al. 2009). There have been no confirmed breeding records of the original wild population after 1991 in Sweden (Tolvanen et al. 2009) and 1995 in Finland (Jones et al. 2008). Because reintroduction initiatives are underway (Jones et al. 2008), we keep the species in our analysis. Rather, we consider it as important to preserve the species' habitat which is according to our assumptions appropriate to sustain viable populations of that species. Second, for the two amphibian gap species, the databases reveal adequate coverage at several Sites of Community Importance on Mallorca and Corsica. Figure 3 shows the number of fully covered, covered, and gap wetland species after reclassifying the two amphibian species as covered (Corsican painted frog) and fully covered (Mallorcan midwife toad).

Figure 3 about here

As many as 2194 out of 2237 total planning units include at least a fraction of a Natura 2000 site. These units, which comprise an area of about 50x50 km or 250,000 ha, contain between 1 and 391 sites varying in size between <1 and 14,835 ha. This illustrates the high fragmentation of the Natura 2000 network on the densely human-populated European continent. About 7 % of all designated Natura 2000 sites are marked as wetlands in the Spatial Wetland Distribution model, 4.3 % are open waters, and another

12 % might serve as suitable for wetland restoration. Overall, 31 % of all recent wetland sites identified through the Spatial Wetland Distribution model are protected under the Natura 2000 system.

Potentials for expanding the network cost-effectively

To ensure that each considered wetland species is adequately covered with at least one viable population, the existing Natura 2000 network would require additional wetland habitats of 3.02 million hectare at a cost of 106.56 million Euro per year. The land area necessary for the cost-effective coverage of at least one viable population for each species is distributed mainly between the four European Union countries Latvia (68.4 %), Finland (19.4 %), Estonia (12.0 %), and Romania (0.2 %) (Figure 5b). Area requirements and corresponding annual land costs of expansion for a range of additional conservation targets are shown in Figure 4. Figure 5 displays priority areas for a cost-effective expansion of the Natura 2000 reserve system for several conservation targets.

Figure 4 and 5 about here

Delineation of suitable sites for an expansion of the Natura 2000 network

We apply the Spatial Wetland Optimization Modeling Project to downscale the estimates on expansion area per wetland type and planning unit from the HABITAT model. This process is illustrated below for the planning unit 2576 in Estonia. The unit is located between the Baltic Sea in the north and the Russian border to the east. The area contains two large Natura 2000 sites in the southern part, Muraka and Puhatu, which cover peatlands and wet forest complexes. For conservation target 1, the HABITAT model proposes to expand the Natura 2000 sites by 34,438 ha of wet forests and by 270 ha of water bodies. Figure 6 shows the selected planning unit with original and expanded wetland conservation areas.

Figure 6 about here

Discussions and conclusions

This study contributes to the complex issue of evaluating the efficiency and effectiveness of existing reserve systems. Two characteristics distinguish this analysis from previous ones. First, we use coarse scale species occurrence data and still seek to be spatially explicit at a resolution of 1 km². Second, we account for persistence by including species-specific habitat size requirements.

Not surprisingly, the existing scheme of protected areas does not represent all considered 70 vertebrate species adequately. Particularly, four wide-ranging wetland bird species and one mammal species are not covered with a viable population. Explicit additional area requirement for gap species is part of the outcome of our model. However, results of any gap analysis depend critically on the applied conservation targets as well as on the quality of the underlying data (Scott et al. 1993; Maiorano et al. 2006). Changes in the dataset, especially in the population densities or the minimum viable population sizes, could cause considerably different results.

We employ a relatively novel method to conduct a detailed gap analysis with coarse scale species occurrence data. Our planning units are about 50 x 50 km in size and reflect the scale of the available occurrence data. The common approach in conservation planning is to select total planning units as priority area for conservation (Tognelli et al. 2008; Williams et al. 2005; Williams and Araujo 2002). Such procedure faces problems especially in Europe with its human-dominated landscape and high habitat fragmentation. There is a considerable scale difference between the dimension of planning units and the land area available for conservation (Araujo et al. 2004; Larsen and Rahbek 2003; Strange et al. 2006). See Cowling et al. (2003) for a discussion of scale-dependency on reserve selection. Suitable habitat areas for the maintenance of biodiversity may be scattered throughout a planning unit. These habitat patches may be insufficient to enable the long-term survival of species and ecosystems. To overcome this problem, our model selects only suitable parts of a planning unit as priority areas for conservation. We integrate high resolution wetland habitat data to adequately represent the habitat composition in each planning unit. The identified habitat areas must meet the minimum critical areas for all preserved species in each planning unit. In case a species' area or habitat type requirement cannot be fulfilled within a single planning unit, further habitat in adjacent planning units is selected. A method to select reserves for species with differential habitat size needs exceeding planning units' areas is also presented by Marianov et al. (2008).

Our approach has several implications which warrant discussion. On the one hand, the analysis may overestimate species coverage inside reserves. First, the coarse data cause uncertainties. We do not know where exactly inside a UTM50 grid cell a species has been recorded and consequently cannot be sure that species match Natura 2000 reserves or proposed sites for expansion (see also Araujo 2004). To assure the species our model regards as covered by the Natura 2000 network are actually present in its protected areas, we validate our results with the Natura 2000 and the EUNIS biodiversity database. In addition, we assume that suitable wetland habitats are sufficient indicators for wetland species occurrence. Thus, we compensate the deficiencies in species occurrence data by the inclusion of highly accurate habitat data. We consider a species protected when its required wetland habitat in a planning unit with recorded occurrences is protected. A second possibility for overestimation of species coverage is due to the relatively large planning units which prevent an explicit representation of each individual Natura 2000 site. The total Natura 2000 area in a planning unit may be built up from many small and scattered reserves which are not in close proximity to each other. Gaston et al. (2008), among others, raised concerns over the extent to which the European reserve systems can maintain biodiversity, given the small size of many protected areas. In our analysis of the Natura 2000 system, it may happen that although minimum area requirements of species are met, these areas are not made up by reserves that are connected in reality. This is especially critical for species with low dispersal abilities such as amphibians and reptiles. However, in the delineation of potential sites for expansion, we are able to address spatial reserve design criterions such as connectivity and compactness.

Our analysis may also underestimate species coverage inside reserves. First, our model may incorrectly classify some of the species as missing because of inaccurate global earth observation data. The species *Discoglossus montalentii,* for example, has occurrence records in five planning units. Within the boundaries of the corresponding Natura 2000 sites, not a single watercourse exists according to the employed global earth observation datasets CORINE (European Environment Agency 2000) and Global Lakes and Wetlands Database (Lehner and Döll 2004). The species fails to meet conservation targets and is recorded as a gap species. The same argument holds for the species *Alytes muletensis* which is also recorded as gap species due to inaccurate habitat specifications. However, most amphibian species would need small ponds or ditches for breeding. At present, these habitats cannot be detected in satellite data. Second, in addition to statutory protected areas under the Natura 2000 framework, there are other European reserves which are not legally recognized but owned or managed by nongovernmental organizations or by private individuals (Gaston et al. 2008). These areas provide additional protection of wetland species of European conservation concern.

There are several limitations of our approach that need to be noted. First, to estimate species-specific minimum critical areas, we need to implement data on population densities and minimum viable population sizes. However, observed population densities may vary substantially or be biased towards regions with high population densities (Schwanghart et al. 2008). Furthermore, we do not assume that the used values represent real minimum viable populations or that defining explicit sizes for persistent populations is possible. Similar to other studies (Kautz and Cox 2001; Verboom et al. 2001; Kerley et al. 2003), we use these proxies as working targets given the lack of better data. Second, for migratory species, we only consider habitat that is necessary during the breeding season. Reasons are data deficiencies for habitat area requirements in the winter habitat and the fact that most migratory species included in our analysis spend the winter outside of Europe and its Natura 2000 sites.

In agreement with other studies evaluating the effectiveness of the Natura 2000 system (Araujo et al. 2007; Maiorano et al. 2007), we find that the existing sites provide a limited degree of protection. To cover all species of European conservation concern adequately, the existing network needs to be expanded. To increase biodiversity benefits of the

Natura 2000 network in a cost-effective manner, the expansion of protected areas should be coordinated across national borders. Further research is required to evaluate the significance of Natura 2000 sites for biodiversity features we did not include in our study, for example invertebrates, plant species, and vegetation communities.

Further, our study does not take the effects of climate change into account. There is little knowledge of the effects of climate change on wetland ecosystem functions, processes, as well as their spatial and temporal distributions and compositions in Europe (Schleupner 2010a). Thus, the ability to project changes of wetland distribution and quality and the consequences for the Natura 2000 system is limited. However, this topic is in the focus of ongoing research activities (Schleupner et al. 2011).

Finally, we would like to note that we do not seek to undermine the significance of Natura 2000 and the many efforts leading to its existence. We rather intend to highlight the problem of population viability in a reserve system built in a highly fragmented and human-dominated landscape. The simulation results identify several distinct hotspots for the expansion of Natura 2000, most of them located in Eastern Europe. As described before, the choice of additional reserve locations is a trade-off between biophysical suitability and economic opportunity cost. Furthermore, the relatively high habitat requirements in Latvia and Romania relate to priority areas for the protection of several wide-ranging raptors identified as gap species (*Aquila clanga*, *Aquila chrysaetos*, and *Pandion haliaetus*). While our model marks a large fraction of the respective planning units as priority area for conservation, it may not be necessary to totally exclude human activities from these areas. A chance would be to manage the matrix around Natura 2000 sites as a functional part of the reserve system (Maiorano et al. 2006, 2007). Where an expansion is not feasible in the near future, the priority regions identified in our study may serve as starting points for such a matrix management. A general guideline for management of the matrix is to increase its structural similarity with adjacent protected habitat patches (Prevedello and Vieira 2010). This could be accomplished by providing financial incentives to the respective land owners, e.g. through agri-environmental schemes (Donald and Evans 2006; Henle et al. 2008). Modern timber harvesting practices that provide more favorable conditions for survival and movement of biodiversity features are an example of successful matrix management (Kohm and Franklin 1997; Mori 2009). Especially large raptors may tolerate restricted types of livestock production (Meyburg et al. 2004) or adjusted forestry (Löhmus 2005).

Acknowledgements

The authors thank the many volunteer fieldworkers who contributed to the species atlas records. We furthermore thank two anonymous reviewers who gave valuable comments on earlier versions of this paper. This study has received financial support from the *Michael Otto Foundation for Environmental Protection*, the cluster of excellence *Integrated Climate System Analysis and Prediction* (CliSAP), and the European Commission through the FP6 projects *European Non-Food Agriculture* (ENFA), *Global Earth Observation – Benefit Estimation: Now, Next and Emerging* (GEOBENE), and the FP7 project *A European approach to GEOSS* (EuroGEOSS).

Appendix A

Wetland species of European conservation concern

Shown are the 70 included species with their proxies for minimum viable population (MVP) sizes measured in reproductive units (RU) (adapted from Verboom et al. (2001)), density data, and habitat types.

				Required (x) and optional (/) habitat types					
Scientific name	**Vernacular name**	**MVP (RU)**	**Maximum density[c] (RU/ha)**	**Peatlands**	**Wet forest**	**Wet grassland**	**Water course**	**Water body**	**Open water[d]**
Amphibians									
Alytes muletensis	Mallorcan midwife toad	200	20				x		
Bombina bombina	Fire-bellied toad	200	20			x		x	
Bombina variegata	Yellow-bellied toad	200	20		/	/		x	
Chioglossa lusitanica	Golden-striped salamander	200	10				x		
Discoglossus galganoi[a]	Iberian painted frog	200	10					x	
Discoglossus montalentii	Corsican painted frog	200	10				x		
Discoglossus sardus	Tyrrhenian painted frog	200	10					x	
Pelobates fuscus insubricus	Common spadefoot	200	10					x	
Rana latastei	Italian agile frog	200	20		x			x	
Salamandrina terdigitata	Spectacled salamander	200	10				x		
Triturus carnifex	Italian crested newt	200	10		/	/		x	
Triturus cristatus	Great crested newt	200	10		/	/		x	
Triturus dobrogicus	Danube crested newt	200	10			/		x	
Triturus karelini	Southern crested newt	200	10					x	
Triturus montandoni	Carpathian newt	200	10		x	/		x	
Triturus vulgaris ampelensis	Smooth newt	200	20		/	/		x	
Reptiles									
Elaphe quatuorlineata	Four-lined snake	120	2			/			
Emys orbicularis	European pond tortoise	120	15					x	
Mauremys caspica	Stripe necked terrapin	120	9						x
Mauremys leprosa	Spanish terrapin	120	9						x
Birds									
Acrocephalus paludicola	Aquatic warbler	200	1.09			x			
Alcedo atthis	Kingfisher	200	0.15						x
Anser erythropus	Lesser white-fronted goose	200	0.127		x				x
*Aquila chrysaetos**	Golden eagle	120	0.0002	/		/			
*Aquila clanga**	Spotted eagle	120	0.000055	/	x	/	/	/	
Ardea purpurea purpurea	Purple heron	120	0.19			x			x
Ardeola ralloides	Squacco heron	200	0.19			x		x	
Asio flammeus	Short-eared owl	200	0.1	/		/			
Aythya nyroca	Ferruginous duck	200	1			x		x	
Botaurus stellaris stellaris	Bittern	200	0.5			x			

Chlidonias hybridus	Whiskered tern	200	0.19			/		x	
Chlidonias niger	Black tern	200	0.19			x		x	
*Ciconia ciconia**	White stork	120	0.001415			x			*x*
*Ciconia nigra**	Black stork	120	0.00018		x				x
Crex crex	Corncrake	200	0.19	/		x	/		
Fulica cristata	Crested coot	200	10			x		x	
Gavia arctica	Black-throated diver	120	0.006					x	
Gelochelidon nilotica	Gull-billed tern	200	0.19			x	x		
Glareola pratincola	Collared pratincole	200	8			x		x	
*Grus grus**	Crane	120	0.00043	/	/	/		/	
Haliaeetus albicilla	White-tailed eagle	120	0.01273		x				x
Hoplopterus spinosus	Spur-winged plover	200	0.3846			x			x
Ixobrychus minutus minutus	Little bittern	200	1.97			x			x
Marmaronetta angustirostris	Marbled teal	200	0.19			x		x	
Milvus migrans	Black kite	120	1.2733						x
Nycticorax nycticorax	Night heron	200	0.19			x			x
Oxyura leucocephala	White-headed duck	200	1.5					x	
*Pandion haliaetus**	Osprey	120	0.0004		/			x	
Pelecanus crispus	Dalmatian pelican	120	0.19			/		x	
Pelecanus onocrotalus	White pelican	120	0.19			/		x	
Phalacrocorax pygmaeus	Pygmy cormorant	200	0.19		/	/		x	
Philomachus pugnax	Ruff	200	1	/		/			
Platalea leucorodia	Spoonbill	120	0.19		/	x		x	
Plegadis falcinellus	Glossy ibis	200	0.19		/	x		x	
Porphyrio porphyrio	Purple gallinule	200	3.3			x		x	
Porzana parva parva	Little crake	200	5			x		/	
Porzana porzana	Spotted crake	200	0.333	/		/			
Porzana pusilla	Baillon´s crake	200	3.5368			x			
Sterna albifrons	Little tern	200	0.19				x	/	
Tadorna ferruginea	Ruddy shelduck	120	10					x	
Tringa glareola	Wood sandpiper	200	0.12	x	/	/			
Mammals									
Castor fiber[b],*	Eurasian beaver	120	0.002		x				x
Galemys pyrenaicus	Pyrenean desman	200	13.89						x
*Lutra lutra**	European otter	120	0.00017						x
Microtus cabrerae	Cabrera's vole	200	57.5			x			
Microtus oeconomus arenicola	Dutch root vole	200	65	/		/	/	/	
Microtus oeconomus mehelyi	Pannonian root vole	200	65	/		/	/	/	
Mustela lutreola	European mink	200	0.083			/	x	/	
*Myotis capaccinii**	Long-fingered bat	200	0.0042						x
*Myotis dasycneme**	Pond bat	200	0.0042					x	

[a] The genus *Discoglossus galganoi* includes *Discoglossus jeanneae*.

[b] For *Castor fiber*, the Estonian, Latvian, Lithuanian, Finnish, and Swedish populations are excluded (according to 92/43/EEC).

[c] Regarding the densities for colonial birds, we differentiate nesting and foraging areas. The foraging area is set to 5 ha per reproductive unit (RU). Regarding the densities of the amphibian species, we assume 10 RU per hectare for solitary species and 20 RU per hectare for gregarious species.

[d] The category open water is introduced for species that need some type of open water habitat.

[*] Wide-ranging species are indicated with an asterisk.

Appendix B

Agricultural land rents for European countries

	Rent for agricultural land [€/ha*a][a]
Austria	244.53
Belgium	151.76
Bulgaria	70.19
Czech Republic	23.17
Denmark	315.00
Estonia	15.76
Finland	152.08
France	109.35
Germany	156.32
Greece	402.98
Hungary	54.56
Ireland	212.76
Italy	248.42
Latvia	8.34
Lithuania	17.14
Luxembourg	150.38
Malta	115.44
Netherlands	396.01
Poland	68.08
Portugal	158.51
Romania	8.58
Slovakia	13.33
Slovenia	86.21
Spain	145.40
Sweden	98.12
United Kingdom	190.34

[a] data derived from Eurostat (averaged data from 1985 to 2006 for Austria, Belgium, Bulgaria, Denmark, Finland, France, Germany, Greece, Hungary, Ireland, Lithuania, Luxembourg, Malta, Netherlands, Poland, Romania, Slovakia, Spain, Sweden, United Kingdom) and Farm Accountancy Data Network (FADN) (data from 2004 for Czech Republic, Estonia, Italy, Latvia, Portugal, Slovenia)

References

Abellán P, Sanchez-Fernandez D, Velasco J, Millan A (2007) Effectiveness of protected area networks in representing freshwater biodiversity: the case of a Mediterranean river basin (south-eastern Spain). Aquat Conserv 17:361-374

Allen CR, Pearlstine LG, Kitchens WM (2001) Modeling viable mammal populations in gap analyses. Biol Conserv 99:135-144

Araujo MB (2004) Matching species with reserves - uncertainties from using data at different resolutions. Biol Conserv 118:533-538

Araujo MB, Lobo JM, Moreno JC (2007) The Effectiveness of Iberian Protected Areas in Conserving Terrestrial Biodiversity. Biol Conserv 21:1423-1432

Balmford A, Bennun L, ten Brink B, Cooper D, Cote IM, Crane P, Dobson A, Dudley N, Dutton I, Green RE, Gregory RD, Harrison J, Kennedy ET, Kremen C, Leader-Williams N, Lovejoy TE, Mace G, May R, Mayaux P, Morling P, Phillips J, Redford K, Ricketts TH, Rodriguez JP, Sanjayan M, Schei PJ, van Jaarsveld AS, Walther BA (2005) The convention on biological diversity's 2010 target. Science 307:212-213

Benayas JMR, de la Montana E (2003) Identifying areas of high-value vertebrate diversity for strengthening conservation. Biol Conserv 114:357-370

Bladt J, Strange N, Abildtrup J, Svenning JC, Skov F (2009) Conservation efficiency of geopolitical coordination in the EU. J Nat Conserv 17:72-86

Brooks TM, Bakarr MI, Boucher T, da Fonseca GAB, Hilton-Taylor C, Hoekstra JM, Moritz T, Olivier S, Parrish J, Pressey RL, Rodrigues ASL, Sechrest W, Stattersfield A, Strahm W, Stuart SN (2004) Coverage provided by the global protected-area system: Is it enough? Bioscience 54:1081-1091

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vie JC & Watson R (2010) Global Biodiversity: Indicators of Recent Declines. Science 328:1164-1168

Catullo G, Masi M, Falcucci A, Maiorano L, Rondinini C, Boitani L (2008) A gap analysis of Southeast Asian mammals based on habitat suitability models. Biol Conserv 141:2730-2744

Ceballos G (2007) Conservation priorities for mammals in megadiverse Mexico: the effciency of reserve networks. Ecol Appl 17:569-578

Cowling RM, Pressey RL, Rouget M, Lombard AT (2003) A conservation plan for a global biodiversity hotspot - the Cape Floristic Region, South Africa. Biol Conserv 112:191-216

Dietz RW, Czech B (2005) Conservation deficits for the continental United States: an ecosystem gap analysis. Conserv Biol 19:1478-1487

Dimitrakopoulos PG, Memtsas D, Troumbis AY (2004) Questioning the effectiveness of the Natura 2000 Special Areas of Conservation strategy: the case of Crete Global. Ecology and Biogeography 13:199-207

Donald PF, Evans AD (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. Journal of Applied Ecology 43:209-218

European Commission, DG Environment (2008) Natura 2000 dataset DG ENV – B2, Nature & Biodiversity, European Commission, BU-9 3/24

European Commission (2007) Life and Europe's wetlands. Restoring a vital ecosystem. Luxembourg

European Commission (2009a) Natura 2000 - Europe's nature for you. Luxembourg

European Commission (2009b) Natura 2000 European Commission DG ENV Newsletter 27

European Commission (2010) Key figures on Europe. Luxembourg

European Environment Agency (2000) CORINE Land Cover 2000 Database, 100 m. http://dataserviceeeaeuint/dataservice. Cited 15 Jan 2010

European Environment Agency (2009) Progress towards the European 2010 biodiversity target. Copenhagen

European Environment Agency (2010) Natura 2000 data - the European network of protected sites. http://www.eea.europa.eu/data-and-maps/data/natura-2000/. Cited 10 Mar 2010

Fearnside PM, Ferraz J (1995) A Conservation Gap Analysis of Brazil Amazonian Vegetation. Conserv Biol 9:1134-1147

Gasc JP, Cabela A, Crnobrnja-Isailovic J, Dolmen D, Grossenbacher K, Haffner P, Lescure J, Martens H, Martínez Rica JP, Maurin H, Oliveira ME, Sofiandou TS, Veith M, Zuiderwijk A (1997) Atlas of amphibians and reptiles in Europe. Collection Patrimoines Naturels edn Societas Europaea Herpetologica, Muséum National d'Histoire Naturelle & Service du Petrimone Naturel, Paris

Gaston KJ, Jackson SE, Nagy A, Cantu-Salazar L, Johnson M (2008) Protected areas in Europe - Principle and practice. In: Ostfeld RS, Schlesinger WH (ed) The Year in Ecology and Conservation Biology 2008. Blackwell Publishing, Oxford, pp 97-119

Gustafson EJ, Parker G (1992) Using an index of habitat patch proximity for landscape design. Landscape Urban Plan 29:117-130

Hagemeijer WJM, Blair MJ (1997) The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. T & A D Poyser, London

Hawths Analysis Tools (2006) http://wwwspatialecologycom/htools. Cited 10 Jul 2009

Henle K, Alard D, Clitherow J, Cobb P, Firbank L, Kull T, McCracken D, Moritz RF, Niemel J, Rebane M, Wascher D, Watt A, Young J (2008) Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe-A review. Agriculture, Ecosystems & Environment 124:60-71

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. Ecol Lett 8:23-29

IUCN (2003) Recommendations of the Vth IUCN World Parks Congress, Durban, South Africa, 8–17, September 2003. http://wwwiucnorg/themes/wcpa/ wpc2003/pdfs/outputs/wpc/recommendationspdf. Cited 10 Mar 2010

Jantke K, Schneider UA (2010) Multiple-species conservation planning for European wetlands with different degrees of coordination. Biol Conserv 143:1812-1821

Jenkins CN, Joppa L (2009) Expansion of the global terrestrial protected area system. Biol Conserv 142:2166-2174

Jones TA, Hughes JMR (1993) Wetland inventories and wetland loss studies: a European perspective. In: Moser M, Prentice RC, van Vessem J (ed) Waterfowl and wetland conservation in the 1990s: a global perspective. Proc IWRB Symp., St Petersburg Beach, Florida, USA. IWRB Spec. Publ. No. 26, Slimbridge, UK, pp 164-169

Jones T, Martin K, Barov B, Nagy S (Compilers) (2008) International Single Species Action Plan for the Conservation of the Western Palearctic Population of the Lesser White-fronted Goose Anser erythropus. AEWA Technical Series No.36, Bonn, Germany

Kautz RS, Cox JA (2001) Strategic habitats for biodiversity conservation in Florida. Conserv Biol 15:55-77

Kerley GIH, Pressey RL, Cowling RM, Boshoff AF, Sims-Castley R (2003) Options for the conservation of large and medium-sized mammals in the Cape Floristic Region hotspot, South Africa. Biol Conserv 112:169-190

Kohm KA, Franklin JF (1997) Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC

Lang S, Tiede D (2003) V-Late Extension für ArcGIS – vektorbasiertes Tool zur quantitativen Landschaftsstrukturanalyse. ESRI Anwenderkonferenz 2003 Innsbruck. Innsbruck, Austria: ESRI, CD-ROM

Larsen FW, Rahbek C (2003) Influence of scale on conservation priority setting - a test on African mammals. Biodiv Conserv 12:599-614

Lehner, B, Döll, P (2004) Development and validation of a global database of lakes, reservoirs and wetlands. J Hydrol 296:1-22

Löhmus A (2005) Are timber harvesting and conservation of nest sites of forest-dwelling raptors always mutually exclusive? Animal Conserv 8:443-450

Maiorano L, Falcucci A, Boitani L (2006) Gap analysis of terrestrial vertebrates in Italy: Priorities for conservation planning in a human dominated landscape. Biol Conserv 133:455-473

Maiorano L, Falcucci A, Garton EO, Boitani L (2007) Contribution of the Natura 2000 Network to Biodiversity Conservation in Italy. Conserv Biol 21:1433-1444

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243-253

Margules CR, Sarkar S (2007) Systematic conservation planning. Cambridge University Press, Cambridge.

Marianov V, ReVelle C, Snyder S (2008) Selecting compact habitat reserves for species with differential habitat size needs. Comput Oper Res 35:475-487

Meyburg BU, Scheller W, Bergmanis U, Chancellor R, Meyburg B (2004) Home range size, habitat utilisation, hunting and time budgets of lesser spotted eagles Aquila pomarina with regard to disturbance and landscape fragmentation. Raptors worldwide:

proceedings of the VI World Conference on Birds of Prey and Owls, Budapest, Hungary, 18-23 May 2003. pp 615-635

Mitchell-Jones AJ, Amori G, Bogdanowicz W, Krystufek B, Reijnders PJH, Spitzenberger F, Stubbe M, Thissen JBM, Vohralík V, Zima J (1999) The Atlas of European Mammals. Academic Press, London

Mori, AS (2009) Forest management for conserving biodiversity: matrix management in Swedish forests. Hozen Seitaigaku Kenkyu 14:283-291

Naidoo R, Balmford A, Ferraro PJ, Polasky S, Ricketts TH, Rouget M (2006) Integrating economic costs into conservation planning. Trends Ecol Evol 21:681-687

Nel JL, Reyers B, Roux DJ, Cowling RM (2009) Expanding protected areas beyond their terrestrial comfort zone: Identifying spatial options for river conservation. Biol Conserv 142:1605-1616

O'Dea N, Araújo MB, Whittaker RJ (2006) How well do Important Bird Areas represent species and minimize conservation conflict in the Tropical Andes? Diversity and Distributions 12:205-214

Oldfield TEE, Smith RJ, Harrop SR, Leader-Williams N (2004) A gap analysis of terrestrial protected areas in England and its implications for conservation policy. Biol Conserv 120:303-309

Pinto M, Grelle C (2009) Reserve selection and persistence: complementing the existing Atlantic Forest reserve system. Biodiv Conserv 18:957-968

Powell GVN, Barborak J, Rodriguez M (2000) Assessing representativeness of protected natural areas in Costa Rica for conserving biodiversity: a preliminary gap analysis. Biol Conserv 93:35-41

Pressey RL, Whish GL, Barrett TW, Watts ME (2002) Effectiveness of protected areas in north-eastern New South Wales: recent trends in six measures. Biol Conserv 106:57-69

Prevedello JA, Vieira MV (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodiv Conserv 19:1205-1223

Pullin AS, Baldi A, Can OE, Dieterich M, Kati V, Livoreil B, Lovei G, Mihok B, Nevin O, Selva N, Sousa-Pinto I (2009) Conservation Focus on Europe: Major Conservation Policy Issues That Need to Be Informed by Conservation Science. Conserv Biol 23:818-824

Ramesh BR, Menon S, Bawa KS (1997) A vegetation based approach to biodiversity gap analysis in the Agastyamalai region, Western Ghats, India. Ambio 26:529-536

Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffmann M, Long JS, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2004a) Effectiveness of the global protected area network in representing species diversity. Nature 428:640-643

Rodrigues ASL, Akçakaya HR, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Chanson JS, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffmann M, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2004b) Global Gap Analysis: Priority Regions for Expanding the Global Protected-Area Network. Bioscience 54:1092-1100

Rondinini C, Pressey RL (2007) Special Section: Systematic Conservation Planning in the European Landscape: Conflicts, Environmental Changes, and the Challenge of Countdown 2010. Conserv Biol 21:1404-1405

Rouget M, Richardson DM, Cowling RM (2003) The current configuration of protected areas in the Cape Floristic Region, South Africa - reservation bias and representation of biodiversity patterns and processes. Biol Conserv 112:129-145

Sarkar S, Pressey RL, Faith DP, Margules CR, Fuller T, Stoms DM, Moffett A, Wilson KA, Williams KJ, Williams PH, Andelman S (2006) Biodiversity conservation planning tools: Present status and challenges for the future. Annu Rev Env Res 31:123-159

Schleupner C (2009) GIS as integrating tool in sustainability and global change. Reports on Earth System Science 62. Max Planck Institute for Meteorology, Hamburg

Schleupner C (2010a) Modelling the Implications of Climate Change for European Freshwater Wetland Distributions: A Review of Knowledge and Gaps. The International Journal of Climate Change: Impacts and Responses 2: http://www.Climate-Journal.com

Schleupner C (2010b) GIS-based estimation of wetland conservation potentials in Europe. In: Taniar D, Gervasi O, Murgante B, Pardede E, Abduhan B (ed) Computational Science and its applications, Part I. Springer, New York, pp193-209

Schleupner C, Jantke K, Schneider UA (2011) Defining areas of regional wetland conservation concern in Europe under environmental and policy change scenarios. Geophysical Research Abstracts 13, EGU General Assembly 2011.

Schwanghart W, Beck J, Kuhn N (2008) Measuring population densities in a heterogeneous world Global. Ecology and Biogeography 17:566-568

Scott JM, Davis F, Csuti B, Noss R, Butterfield B, Groves C, Anderson H, Caicco S, Derchia F, Edwards TC, Ulliman J, Wright RG (1993) Gap Analysis - A Geographic Approach to Protection of Biological Diversity. Wildlife Monogr 123:1-41

Scott JM, Davis FW, Mcghie RG, Wright RG, Groves C, Estes J (2001) Nature reserves: Do they capture the full range of America's biological diversity? Ecol Appl 11:999-1007

Shaffer ML, Stein BA (2000) Safeguarding our precious heritage. In: Stein BA, Kutner LS, Adams JS (ed) Precious Heritage: The status of biodiversity in the United States. Oxford University Press, Oxford, pp 301-321

Smith G, Gillett H (2000) European Forests and Protected Areas: Gap analysis. UNEP World Conservation Monitoring Centre, Cambridge

Sowa SP, Annis G, Morey ME, Diamond DD (2007) A gap analysis and comprehensive conservation strategy for riverine ecosystems of Missouri. Ecol Monogr 77:301-334

Strange N, Rahbek C, Jepsen JK, Lund MP (2006) Using farmland prices to evaluate cost-efficiency of national versus regional reserve selection in Denmark. Biol Conserv 128:455-466

Tiede D (2005) V-Late – Vector-based Landscape Analysis Tools. http://wwwgeosbgacat/larg/vlatehtm. Cited 20 Dec 2009

Tognelli MF, de Arellano PIR, Marquet PA (2008) How well do the existing and proposed reserve networks represent vertebrate species in Chile? Diversity and Distributions 14:148-158

Tolvanen P, Øien IJ, Ruokolainen K (eds) (2009) Conservation of Lesser White-fronted Goose on the European migration route. Final Report of the EU LIFE-Nature project 2005-2009. WWF Finland Report 27 & NOF Rapportserie Report No 1-2009

Verboom J, Foppen R, Chardon P, Opdam P, Luttikhuizen P (2001) Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. Biol Conserv 100:89-101

Weber N, Christophersen T (2002) The influence of non-governmental organisations on the creation of Natura 2000 during the European Policy process. Forest Policy and Economics 4:1-12

Williams J, ReVelle C, Levin S (2005) Spatial attributes and reserve design models: A review. Environ Model Assess 10:163-181

Williams PH, Araujo MB (2002) Apples, oranges, and probabilities: Integrating multiple factors into biodiversity conservation with consistency. Environ Model Assess 7:139-151

Yip JY, Corlett RT, Dudgeon D (2004) A fine-scale gap analysis of the existing protected area system in Hong Kong, China. Biodiv Conserv 13:943-957

Table 1. Wetland areas inside and outside Natura 2000 sites

	wetland category	inside Natura 2000 [in 1,000 ha]	outside Natura 2000 [in 1,000 ha]
recent wetland	peatlands	3,267.7	5,862.5
	wet forest	1,535.9	4,849.2
	wet grassland	246.3	523.8
potential wetland restoration area	peatlands	5,772.6[a]	41,495.3
	wet forest	3,617.3[a]	24,010.9
	wet grassland	4,408.1[a]	21,122.4
	total[b]	8,865.3	59,301.7
open water	water body	2,773.4	6,557.8
	water course	401.3	519.5

[a] Potential wetland restoration areas from the Spatial Wetland Distribution model inside Natura 2000 sites are given for illustration purposes here, but are not included in the analysis.

[b] In the Spatial Wetland Distribution model all three wetland types of the potential wetland restoration areas are allowed to overlap. The total area of potential sites is therefore not a summation of all wetland types.

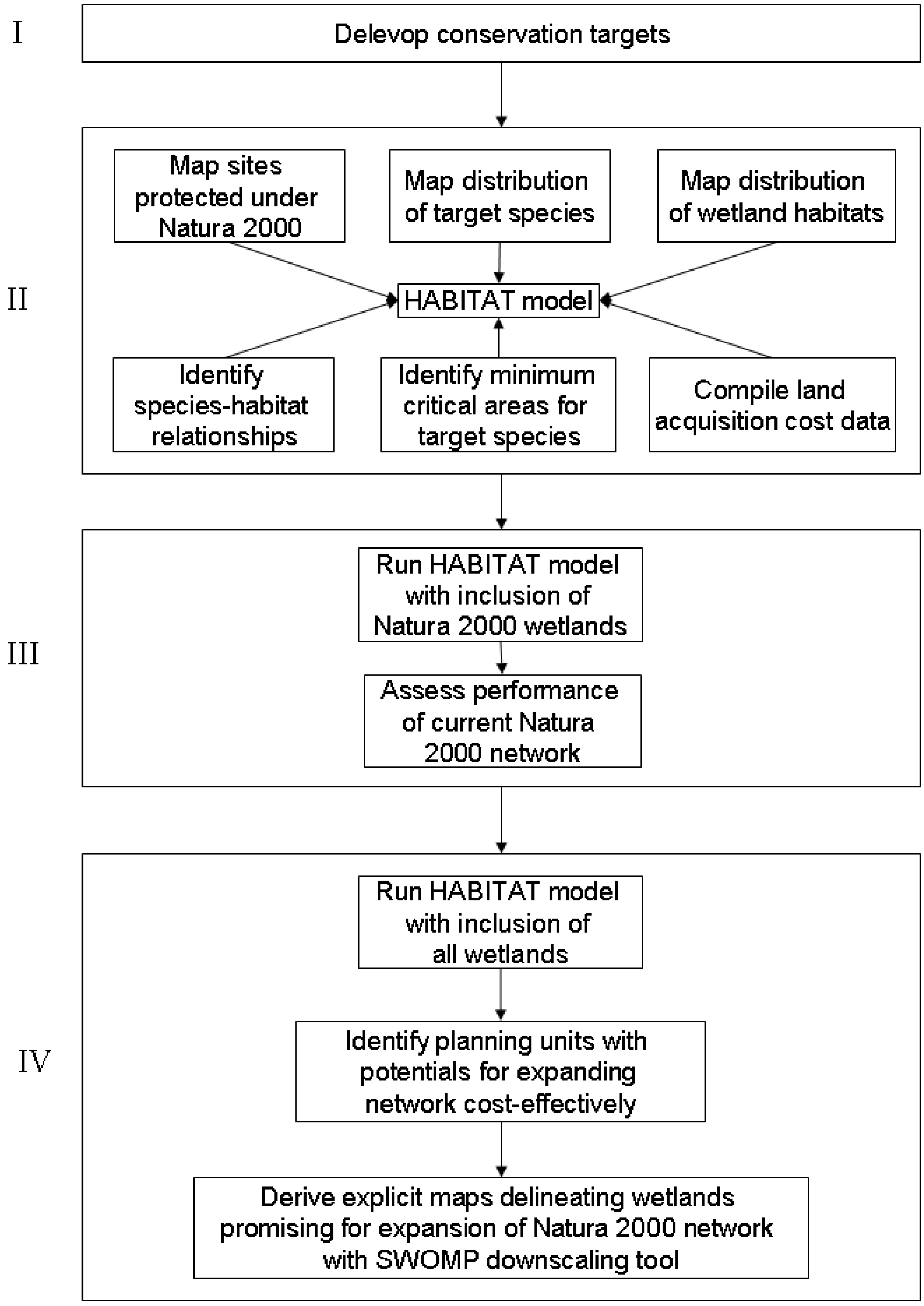

Figure 1: Flowchart of steps used to perform a gap analysis of European wetland species

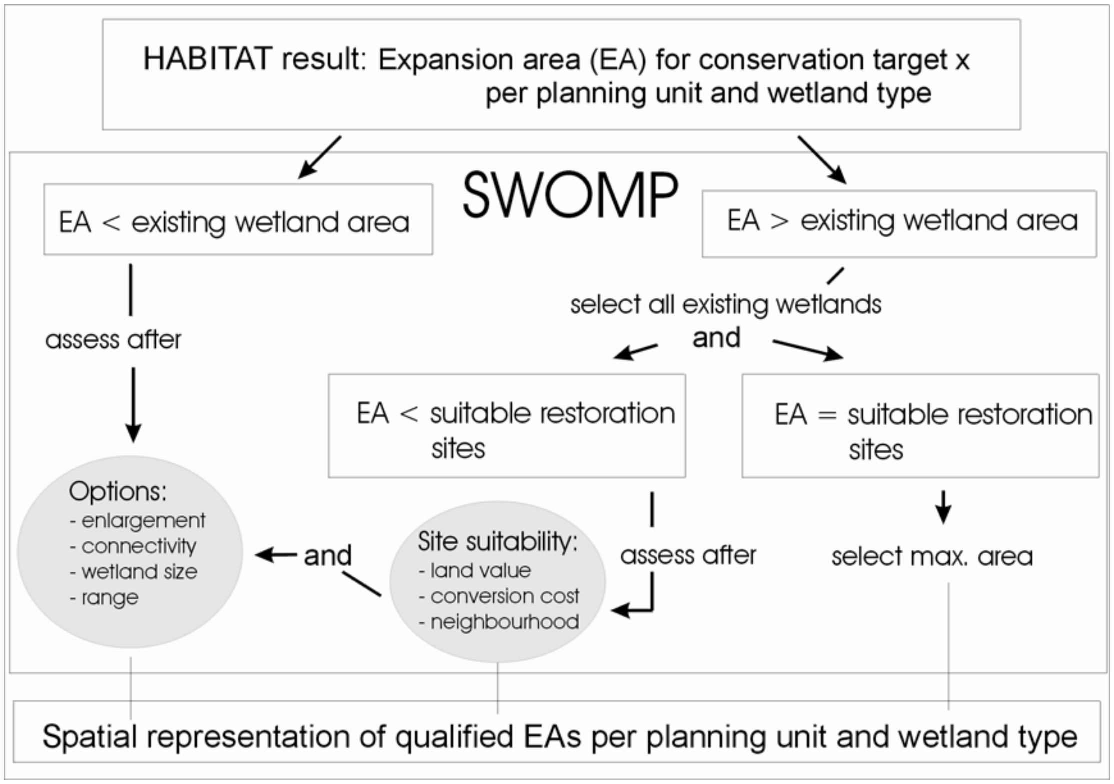

Figure 2: Overview of the downscaling tool SWOMP

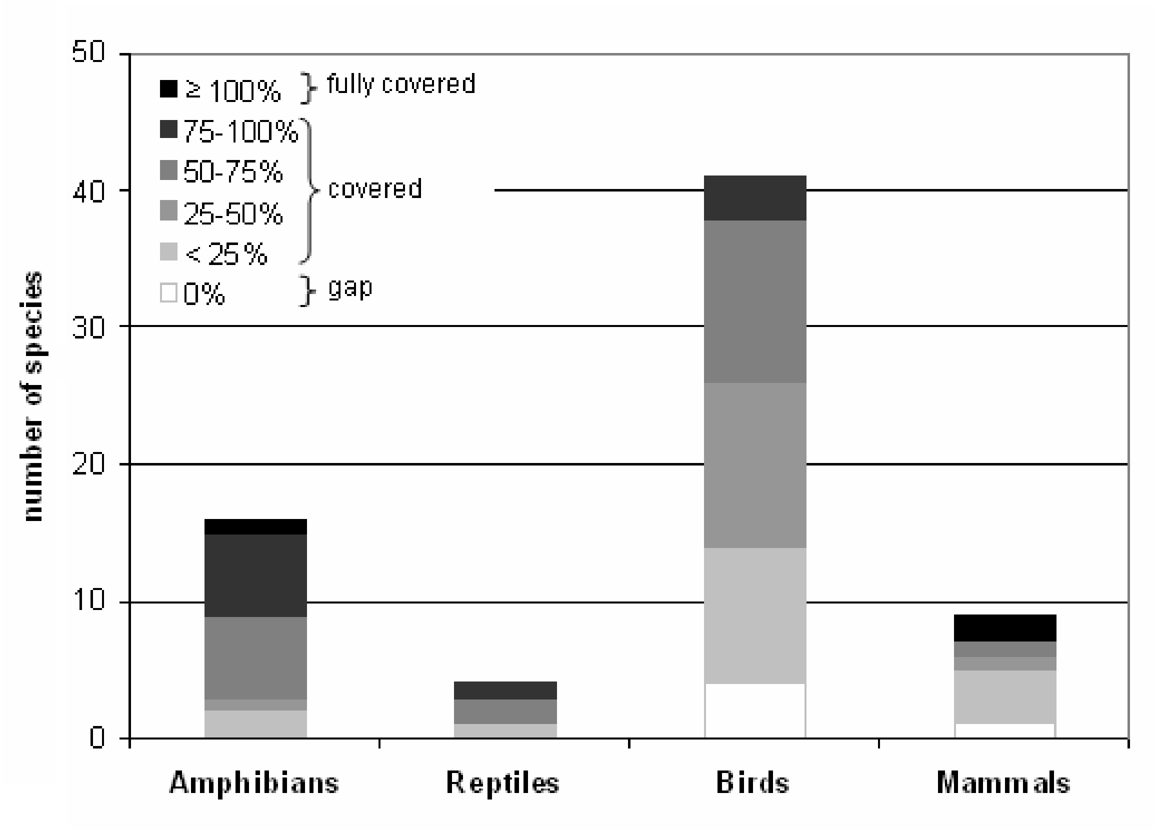

Figure 3: Number of fully covered, covered, and gap wetland species. Percentages indicate the degree of recorded occurrences covered by the Natura 2000 network

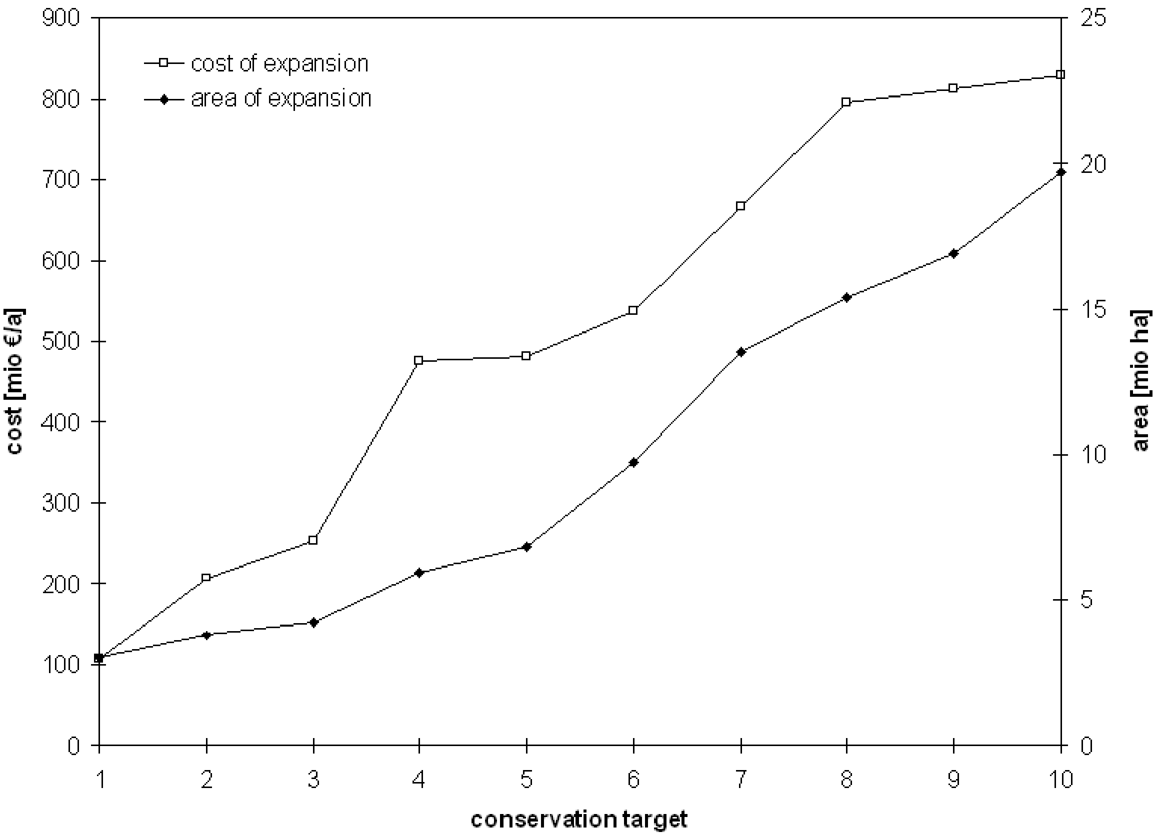

Figure 4: Additional cost and area requirements of an expanded Natura 2000 network for conservation targets 1 to 10

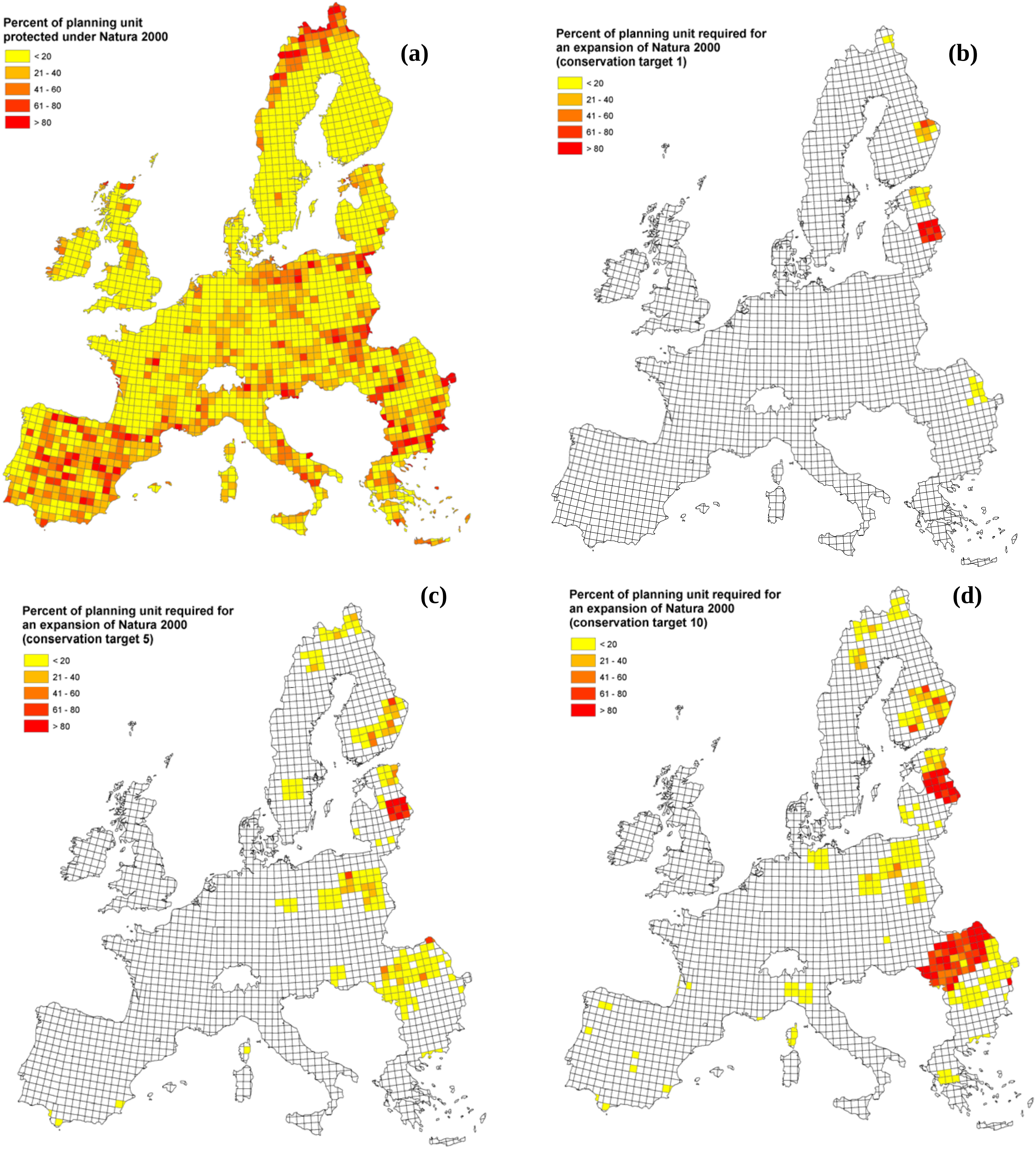

Figure 5: Priority areas for wetland conservation in Europe. a: current protection levels under Natura 2000; b-d: priority areas for an expansion of Natura 2000 for conservation targets 1, 5, and 10.

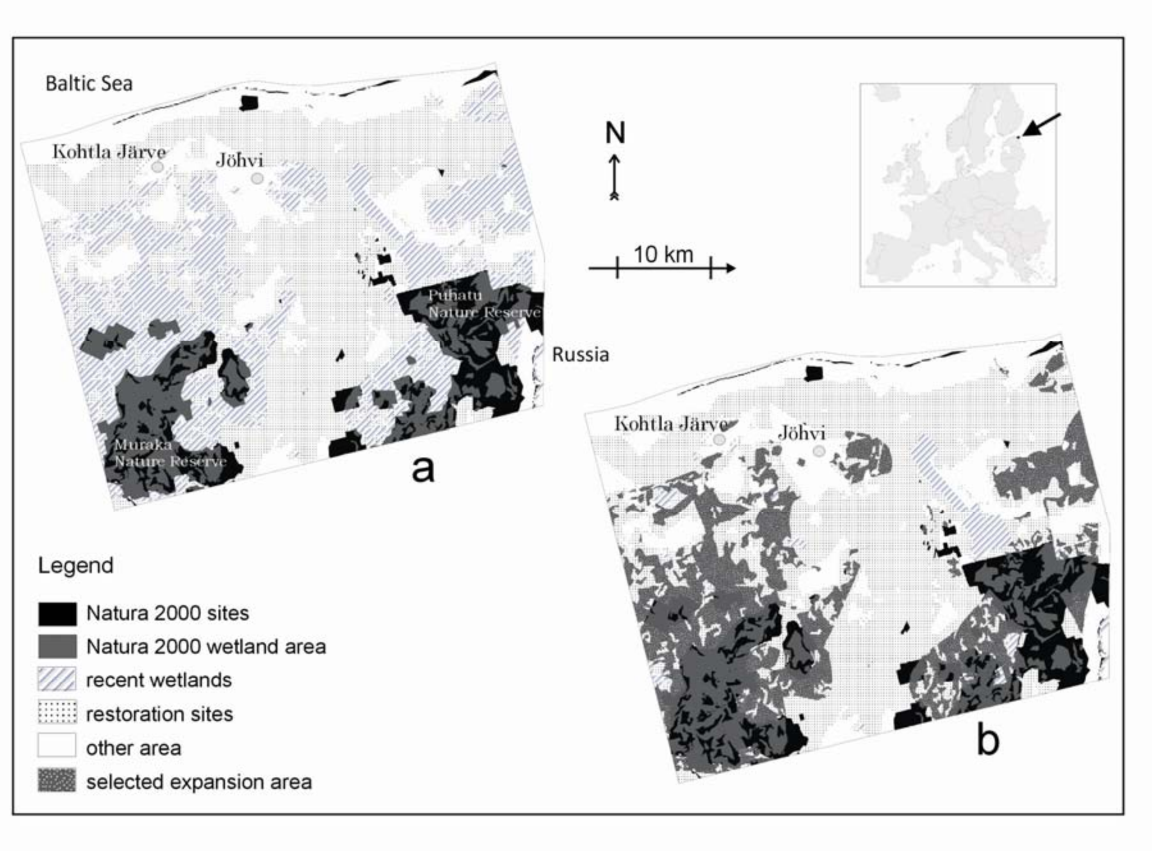

Figure 6: Downscaling example for planning unit 2576 in Estonia. a: current Natura 2000 and wetland distribution; b: SWOMP results based on HABITAT outcomes for conservation target 1