Misleading results from conventional gap analysis – Messages from the warming north

Heini Kujala [a,*], Miguel B. Araújo [b,c], Wilfried Thuiller [d], Mar Cabeza [a,b]

[a] Metapopulation Research Group, Department of Biosciences, P.O. Box 65, 00014 University of Helsinki, Finland
[b] Biodiversity and Global Change Lab, Museo Nacional de Ciencias Naturales, CSIC, C/ José Gutiérrez Abascal 2, Madrid 28006, Spain
[c] Rui Nabeiro Biodiversity Chair, CIBIO, Universidade de Évora, Largo dos Colegiais, 7000 Évora, Portugal
[d] Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France

ARTICLE INFO

ABSTRACT

Gap analysis is a widely used method for assessing the representation of species in protected area (PA) networks. However, representation does not imply persistence. Here, we investigated whether gap analysis may result in misleading conservation guidelines by comparing the representation to two indicators of persistence. We ran a gap analysis with Finnish breeding birds and identified conservation priorities based on current distribution patterns. We tested the sensitivity of these results by using two target setting schemes and several thresholds defining the amount of protected area, and found the levels of representation identified by gap analysis to be robust. We then compared the gap analysis results with recent population trends and projected changes in potential suitable climate under different climate change scenarios for the year 2050. We show that although high latitude species are well represented in PAs, they are currently declining and are projected to lose climatic suitability in the near future. In contrast, low latitude species with poor representation in PAs have increasing population trends and are generally expected to expand their ranges into protected areas in the near future. This study demonstrates with empirical data a mismatch between representation in PAs and population trends, resulting in misleading understanding of current PA effectiveness. The mismatch is linked to the latitude of species distributions and corresponds to expected future changes, indicating that the patterns are potentially driven by climate change. We therefore urge practitioners and researchers to include better indicators of persistence in gap-analysis frameworks even for short term assessments.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

Gap analysis is a conservation tool designed to assess the representativeness of existing protected area networks and to identify conservation priorities (Jennings, 2000; Margules and Pressey, 2000; Scott et al., 1993). It has been used at a variety of scales (e.g. Rodrigues et al., 2004a; Sowa et al., 2007), gaining popularity in scientific studies (e.g. 220 publications since 1992), as well as in practical assessments (GAP, 2010; Langhammer et al., 2007). Gap analysis is essentially a comparison of the distributions of species (or any other feature of conservation interest) with that of protected areas, used to define the degree to which species are represented in the protected areas, and to compare the representations to prescribed targets (Margules and Pressey, 2000; Scott et al., 1993). Species can then be classified as *true gap species* – species not represented in any of the protected areas; *partial gap species* – species underrepresented in protected areas, thus not achieving

the targets set for them; and *covered species* – species that are represented in the protected areas and that achieve their targets (e.g. Rodrigues et al., 2004a,b). The main outcome of gap analysis is to identify the true or partial gap species which need further protection. Species identified as covered are assumed to be well protected. Although this information can be used to guide the selection of new protected areas, gap analysis per se does not prescribe methods for protected area design and is not a primary tool for selecting new areas for conservation. One fundamental assumption behind gap analysis is proactive conservation, i.e. not to focus only on rare species but also on common species. This is believed to be more cost-efficient (Scott et al., 1987) and exhibit a higher probability of success (Tear et al., 1993) than trying to save species when they are on the brink of extinction.

Gap analysis has known shortcomings. Like any other conservation planning analysis, the coarseness and/or correctness of data can influence the results (Hulbert and Jetz, 2007; Rondinini et al., 2006). A further source of uncertainty can arise from mismatching resolutions of species and protected areas data (Araújo, 2004). Thus, the true representation of biodiversity features in protected

---

* Corresponding author. Tel.: +358 9 191 57922; fax: +358 9 191 57694.
E-mail address: heini.kujala@helsinki.fi (H. Kujala).

areas often cannot be guaranteed (Jennings, 2000) and more detailed surveys are needed for fine-tuning the results before prioritization can be made (Jennings, 2000; Scott et al., 1993). This is closely followed by the question of what is an adequate representation level and whether it is even possible to determine one (Jennings, 2000; Rodrigues et al., 2004b). By focusing exclusively on species presence or absence in protected areas, gap analysis does not explicitly account for future threats nor does it assess the long-term persistence of biodiversity in protected areas (Cabeza and Moilanen, 2001). However there is no reason why gap analysis cannot incorporate assessments of the long-term changes in species distributions and studies have already been undertaken by looking at expected species distribution shifts under climate change (e.g. Dockerty et al., 2003; Hannah et al., 2007). Despite these shortcomings, gap analysis is widely used because it offers a simple, quantitative, and standardized method for evaluating the representativeness of protected area networks. But in a rapidly changing world, what conclusions could be drawn from gap analysis based on observed species distribution data and how should it be used when evaluating priorities for conservation?

In this paper, we evaluate existing protected areas in Finland and demonstrate how conventional gap analysis using distribution data for breeding birds results in potentially misleading conservation guidelines. We do a gap analysis to evaluate representation of Finnish breeding birds, and compare the results to two indicators of persistence: recent population trends from the past ca. 25 years and projections of distributional shifts under climate change scenarios. Population trends are a dynamic measure of the status of species, which correlate strongly with extinction risk (O'Grady et al., 2004) and can act as an indicator of conservation success (Donald et al., 2007). Future changes are more difficult to anticipate, but out of all processes that can negatively affect biodiversity, climate change will very likely take place regardless of our current actions (IPCC, 2007). Several techniques are available to project some of the impacts of climate change, especially for projecting species potential distributional shifts (e.g. Guisan and Thuiller, 2005; Heikkinen et al., 2006). We thus evaluate the potential future impacts of climate change on bird distributions, using projections from bioclimatic envelope models for 2050.

These analyses allow us to evaluate (i) what are the representation gaps in the current protected area network; and (ii) how does the representation in current protected areas correspond to short term persistence (i.e. population trends) or to (iii) long term persistence (i.e. projections).

2. Material and methods

2.1. Gap analysis

The bird data are based on the combined information of the first and second Finnish Bird Atlases (Hyytiä et al., 1983; Väisänen et al., 1998), which have been compiled from bird surveys done during 1974–1979 and 1986–1989. The combined atlas contains an index of breeding probability (ranging from 0 = not found; to 4 = confirmed breeding) of 248 bird species on a 10 km × 10 km uniform grid that covers nearly the entire area of Finland (totaling 3813 grid cells). The species fall into 10 groups according to their preferred habitat (Väisänen et al., 1998, and Table 1). We excluded all species pertaining to agricultural and built-up areas (n = 38), as protected areas are not expected to be the means to protect them. We also excluded *Anser caerulescens* (snow goose) because of its unclear status as a wild bird species in Europe (R.A. Väisänen, personal communication). The breeding probabilities of the remaining 209 species were then converted into presence/absence data by defining a species to be absent in cells where probability of

Table 1
Proportions of true gap, partial gap and covered species in each habitat group based on the 20% threshold for protected cells and using two target setting schemes (see Section 2.1). Classification and numbering of groups follow Väisänen et al. (1998) except for the group lakes and seas, which includes both species of Baltic archipelago and coasts, and species of oligotrophic lakes from Väisänen et al. (1998).

Habitat				
Target scheme	Gap	Partial gap	Covered	n
0. Lakes and seas				46
$T_{(a)}$	4.3	58.7	37.0	
$T_{(t)}$	4.3	60.9	34.8	
1. Forest generalists				15
$T_{(a)}$	0.0	60.0	40.0	
$T_{(t)}$	0.0	66.7	33.3	
2. Coniferous forests				28
$T_{(a)}$	3.6	71.4	25.0	
$T_{(t)}$	3.6	78.6	17.9	
3. Old-growth forests				15
$T_{(a)}$	0.0	66.7	33.3	
$T_{(t)}$	0.0	86.7	13.3	
4. Deciduous forests				19
$T_{(a)}$	15.8	78.9	5.3	
$T_{(t)}$	15.8	78.9	5.3	
5. Bushes and saplings				13
$T_{(a)}$	23.1	76.9	0.0	
$T_{(t)}$	23.1	76.9	0.0	
7. Open peatlands				19
$T_{(a)}$	0.0	10.5	89.5	
$T_{(t)}$	0.0	36.8	63.2	
8. Arctic mountains				21
$T_{(a)}$	0.0	9.5	90.5	
$T_{(t)}$	0.0	23.8	76.2	
9. Wetlands				33
$T_{(a)}$	18.2	66.7	15.2	
$T_{(t)}$	18.2	66.7	15.2	

Target setting schemes: $T_{(a)}$ = Distribution area, $T_{(t)}$ = Threat categories.

breeding was unlikely or the species was not observed (classes 0 and 1), and present if the probability was possible or higher (classes 2–4).

The protected area network data include coordinates and spatial configuration of 3148 protected areas, national parks and wilderness areas representing 94.3% of the total area of the Finnish protected area network (36,942 km²) (Fig. 1a). The data were compiled in an earlier project and are a combination of polygons extracted from the WDPA 2005 (World Database on Protected Areas, IUCN and UNEP, 2005) and from the archives of the Finnish Environmental Institute (see details in Appendix A). Although more recent versions of WDPA are available, we have found that there are still considerable errors in the records for Finland such as missing areas (especially in North-Finland), wrongly shaped sites and duplicated records even in the newest version of 2011. After careful comparisons we have concluded that the protected area network data used in this study is more accurate than the one provided by WDPA alone and therefore provides a more comprehensive representation of the existing network.

All records that included discontinuous sites were divided into individual protected areas and adjacent protected areas were joined and considered as single protected areas, increasing the number of sites to 6613. Following the steps of Rodrigues et al. (2004b), we excluded from the analyses all sites smaller than 1 km² (100 ha) as they are likely to have a negligible role in conserving intact communities of vertebrate species (although they may play other important roles within a protected area network, for discussion see Rodrigues et al., 2004b; Gurd et al., 2001). Areas designated as gray seal reserves (n = 5) were also excluded because they are mostly open water. Exclusion of gray seal reserves and
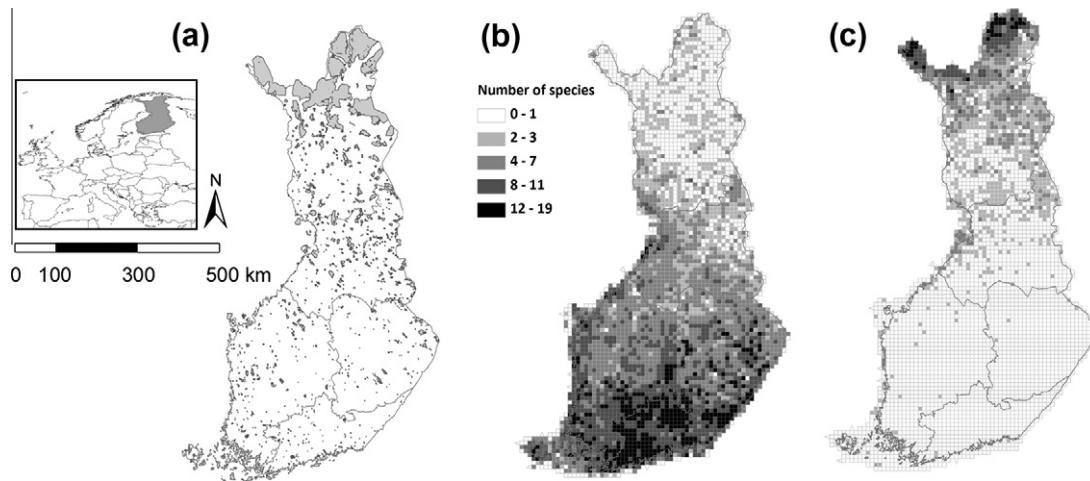
Fig. 1. Maps of the protected areas included into the analyses (a) and species richness within deciduous forest (b) and arctic mountains (c) habitat groups. Maps (b) and (c) illustrate latitudinal differences in species richness between some of the habitat groups.

sites smaller than 1 km² eliminated 84.5% of the site records but decreased the overall area protected by only 1.75%. These modifications resulted in a total of 1025 site records (median size 35.4 km², ranging from 1 km² to 7010 km²), hereafter referred to as protected areas. We transformed the protected area data into raster format by overlaying the polygons on a uniform 10 × 10 km grid corresponding to the grid used in the Finnish Bird Atlas, and defining a grid cell to be protected if 20% of its area overlapped with protected areas. We also conducted a sensitivity analysis by repeating the gap analysis with different values for the minimum percentage of overlap (5%, 10%, 15% and 50%, respectively, see Appendix A and Fig. A.2).

We used two common approaches for setting a priori representation targets for each species. In our first approach targets were set based on species distribution size. Species with narrow distributions (area occupied ⩽500 km²) were assigned a representation target of 100%, meaning that their entire distribution should be protected for them to be considered as covered. Widespread species (area occupied ⩾25,000 km²) were assigned a target of 10% and target coverage for species with intermediate distribution sizes was scaled between the two extremes using a linear regression on the log of area occupied (Fig. A.4). We used sliding targets because a fixed target (e.g. 10%) would mean that larger areas of common species should be protected in comparison to rare and/or narrowly distributed species, which is not desirable (for discussion see e.g. Rodrigues et al., 2004a,b).

Although target setting based on distribution size is a common practice in gap analyses, on a national scale it can give biased results. This is because very narrowly distributed species can simply be on the edges of their distributions in one country, but widespread and common in neighboring countries. Therefore we also used an approach where targets were set based on species' threat categories. We used both national (Finnish Red List, Rassi et al., 2001) and European (SPEC, BirdLife International, Tucker and Heath, 1994) threat categories to calculate a threat weight which was then used to guide the target setting:

$$w_j^T = (pW_j^E + (1 - p)W_j^N),\qquad(1)$$

where W_j^E and W_j^N are weights for species' European and national threat status, respectively, and $p \in [0, 1]$ is a parameter defining the balance between European and national threat weightings (Appendix B). The European threat weights ranged from 1 (Non-SPEC, favorable conservation status, species not concentrated in Europe) to 5 (SPEC1, European species of global conservation concern). The national weights ranged from 1 (not red listed, including IUCN categories NE, DD and LC) to 6 (regionally extinct). For parameter p, defining the balance between W_j^E and W_j^N, a value of 0.3 was used throughout the study to give slightly more weight to the national threat status over the European one. The weights, w_j^T, varied from 1.0 to 5.7, with an average of 1.7. Representation targets were set to 100% for species with very high weights ($w_j^T \geqslant 3.3$), to 10% for species with very low weights ($w_j^T \leqslant 1.6$), and for species with weights in between the target was again interpolated between the two extremes using a log-linear regression.

After setting the targets, we overlaid the filtered, grid transformed protected area data and the presence/absence atlas maps of species to calculate the proportion of distribution protected for each species. Species not represented in any of the protected cells were considered as true gap species, while species that met only a portion of their representation targets were considered as partial gap species.

2.2. Population trends

Population trend data have been collected through national surveys since 1983 and used by Väisänen (2005, 2006) and Hario and Rintala (2007, 2008) to calculate TRIM indices (TRends and Indices for Monitoring Data) for 96 common bird species, some species having several indices from different publication years. Such indices describe the percent annual change in population size relative to the starting year of the monitoring (Pannekoek and van Strien, 2004). We used these published results as our trend data to compare them with the outcomes of our gap analysis. We excluded again all species of agricultural and built-up areas (n = 20) as well as another six species for which, according to Väisänen (2006), the population trends did not properly reflect the long-term changes in population size. The remaining data included 43 species with population trends significantly different from zero (TRIM index varying between −4.6 and 8.6), and 25 species with non-significant trends (TRIM index varying between −3.3 and 2.0) that were assigned a trend value of zero. Note that the non-significance can be due to either true lack of trend or to small sample sizes. Therefore, setting all the non-significant indices to zero can bias the results as some species would be incorrectly treated as having no trend (e.g. Gregory et al., 2009). Because the source data did not allow us to differentiate between the two potential cases, we performed all statistical tests both with and without the non-significant trends. As the accuracy of surveying birds varies among

species (e.g. rare, night-active or elusive species are harder to detect during counts), it is important to note here that these trends do not represent a random sample of the entire species pool, but are biased towards fairly common and day-active species occurring in large areas and/or large populations.

2.3. Projections of bird distributions

Expected changes in the size of the potential distributions of species under climate change were estimated by computing the difference between the projected distributional area of each species in the future and current (baseline) conditions. Although we estimated the changes for Finland alone, the potential distributions were modeled including the whole of the species' European distributions to reduce problems associated with modeling distributions that include incomplete characterizations of species-climate relationships (e.g. Thuiller et al., 2004). Bird species distributions in Europe (from the EBCC European Bird Atlas data, Hagemeijer and Blair, 1997) were modeled following an ensemble forecasting protocol (reviewed by Araújo and New, 2007), and using four techniques implemented in the *BIOMOD* package in R (Thuiller et al., 2009): (1) generalized linear models (GLM), (2) generalized additive models (GAM), (3) classification tree analysis (CTA), and (4) feed-forward artificial neural networks (ANN). Models were calibrated on a 70% random sample of the observed data and the internal verification of the models was performed using the remaining 30% of the data. Note that because the data used for verification of the models are not statistically independent from the calibration data, the evaluation is not one of predictive accuracy but one of internal consistency of the models (Araújo et al., 2005). We tested agreement between observed and projected current distributions by calculating the area under curve (AUC) of the receiver operating characteristic (Roc) curve and Cohen's Kappa statistic (K) (Fielding and Bell, 1997). We used the Kappa approach after maximizing the statistic over a range of thresholds above which model outputs are considered to represent species presence. We calculated AUC using the nonparametric method based on the derivation of the Wilcoxon statistic (Fielding and Bell, 1997). These two approaches were further used to transform probability values from the models into binary presence-absence data (for a review see Liu et al., 2011). Modeling was conducted with available species distributions data for Europe on a UTM (Universal Transverse Mercator) 50×50 km grid, and modeled species potential distributions were projected back onto the 10′ latitude longitude grid for current and future climate. Baseline climate data (1961–1990, CRU CL 2.0 and CRU CL 2.1 dataset) were obtained from the Climatic Research Unit (New et al., 2002; Mitchell et al., 2003; www.cru.uea.ac.uk) and included mean annual, winter, and summer precipitation, mean annual temperature and minimum temperature of the coldest month (MTC), growing degree days (>5°) and an index of moisture availability (for more details see Araújo et al., 2006; Thuiller et al., 2005). Future expected species ranges by 2050 were derived using CRU TYN SC 1.0 dataset (Mitchell et al., 2003) for one climate model (HadCM3, TAR) and four emission scenarios (A1FI, A2, B1 and B2) (Nakicenovic and Swart, 2000). Although it has been argued that using different climate models can lead to differences in modeling outcome, it has also been shown that for projections by 2050 the uncertainties arising from different global climate models are clearly smaller compared to uncertainties associated with different niche models (Buisson et al., 2010; Diniz-Filho et al., 2009). Overall, we obtained 8 baseline (four modeling techniques × two rules for transforming probabilities into presence records) and 32 future (four modeling techniques × two transformations × four climate scenarios) projections for each one of the species modeled.

For calculating the expected future change in the distributional area we used only species for which we had population trend data

(n = 68), further excluding species of lakes and seas (n = 9) as their modeled present distributions differed greatly from their known distributions. We created ensemble maps for each one of the remaining 59 species by overlaying the 8 presence-absence distributions for each time step and scenario, and defining a species to be present in a cell if 6 or more of the models indicated presence. We then calculated the overall difference in the number of occupied cells between the baseline period and each future scenario.

We also calculated the modeled change in the occupancy of those cells that were defined as protected, reflecting the expected change in species distributions within the protected area network. To do this, we first re-sampled the modeled ensemble distributions to match the Finnish atlas grid. We overlaid the two grids and, for each species, calculated the summed percentage of overlap of occupied European grid cells in each of the atlas grid cells. The overlap was then used as the probability for the species to occur in the atlas cells. Finally, we summed the probabilities in the cells defined as protected for each species and calculated the difference between the sums for present and future (Appendix A).

3. Results

The gap analysis identified 20 true gap species (8% of all species analyzed) with no coverage in protected areas when using the 20% threshold to differentiate between protected and unprotected cells. A further 117–132 species (approximately 56–63%), did not achieve the assigned representation depending on the target setting scheme and were identified as partial gaps. The analysis also revealed a clear difference in the level of representation of species from different habitat types (Table 1 and Fig. A.3). A very low proportion of species of southern habitats, i.e. deciduous forests, wetlands and bushes and saplings (Fig. 1b), achieved their targets (5%, 15% and 0%, respectively) and a high proportion was identified as true gaps with zero protection (16%, 18% and 23%, respectively). On the other hand, species of northern habitats (peatlands and arctic mountains, Fig. 1c) had no true gaps and approximately 63–90% of the species achieved the conservation targets assigned to them.

The two target setting schemes allocated targets differently across species, without altering much the overall frequency distribution of targets (Figs. A.5 and A.6). In general, targets were less well met when they were set based on threat categories in comparison to distribution size. However, the two schemes did not result in qualitatively different outputs of the gap analysis, both identifying the same groups of best and worst represented species (Table 1). The results were not very sensitive either to the protected area thresholds used (i.e. 5%, 10%, 15% and 50%), although some differences can be seen in coverage of different habitat groups (see Appendix A). The coverage of northern habitat types was high at all threshold levels, whereas the coverage of southern habitats was at its best at small threshold levels, and low at higher threshold levels.

Compared to the gap and covered species identified by the gap analysis, the population trends of common species generally showed an opposite pattern. Species of the two well represented groups of peatland and arctic mountain habitats tended to have strongly declining population trends for the past 25 years (Fig. 2a), whereas species of one of the poorly represented groups, deciduous forest habitat, tended to have strongly increasing population trends. The population trend data also reveal that roughly one third of the species not achieving their targets were associated with increasing trends, whereas species surpassing their targets had only stable or declining trends (Fig. 3). We found a significant negative linear correlation between population trend and the proportion of representation target achieved in gap analysis when targets were assigned based on distribution size (Spearman
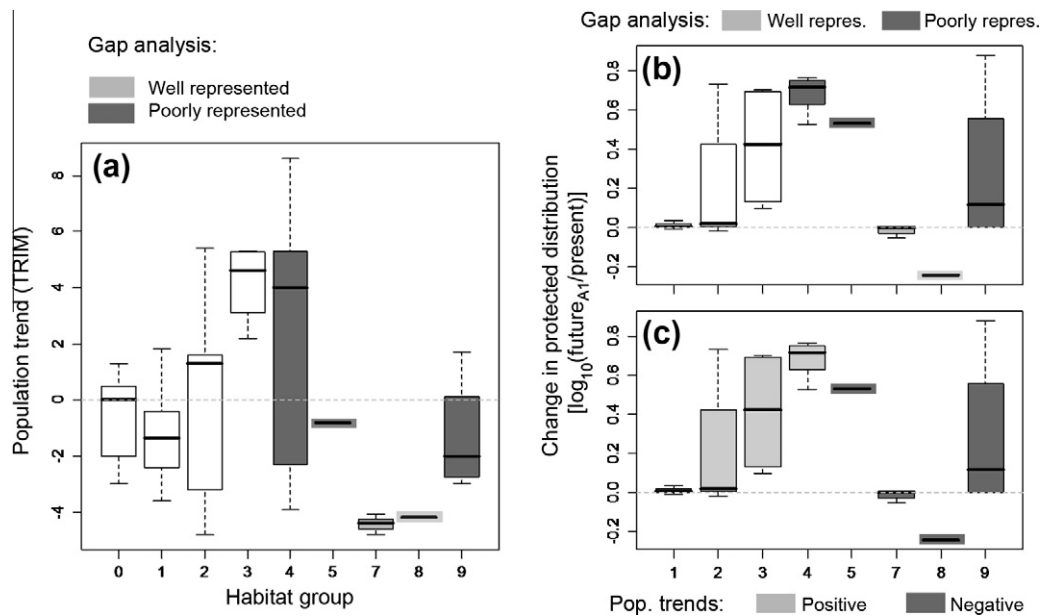
Fig. 2. Comparison of gap analysis results, population trends and expected change in protected distribution in each of the habitat groups. (a) Population trends in each habitat group, the horizontal lines representing the median within group. Groups that are in general well or poorly represented based on the gap analysis are colored accordingly. (b) Expected change in the size of protected distribution in each habitat group, measured as the logarithmic ($\log_{10}$) relation of protected area in the year 2050 under the emission scenario A1 to protected present area. Positive and negative values indicate an expected increase and decrease in the size of protected distribution by the year 2050 respectively. Groups have been colored on the basis of gap analysis results (upper graph) and population trends (lower graph, positive or negative status defined by the median population trend in each group). Habitat groups: 0 = Lakes and seas, 1 = Forest generalists, 2 = Coniferous forests, 3 = Old-growth forests, 4 = Deciduous forests, 5 = Bushes and saplings, 7 = Open peatlands, 8 = Arctic mountains, 9 = Wetlands.

correlation *rho* (ρ_{with}) = −0.367, *P* = 0.002 with non-significant trends, and *rho* (ρ_{without}) = −0.505, *P* < 0.001 without) (Fig. 3a). When targets were based on threat categories the correlation was weaker (ρ_{with} = −0.211, *P* = 0.084; ρ_{without} = −0.240, *P* = 0.1206) but there was nonetheless a steep decline in population trend when targets were met in increasing proportions (Fig. 3b, see also Fig. A.7). Looking at the weighted centers of occurrences (from Hyytiä et al., 1983) of each species, we found that the opposing pattern is linked to the latitude of species distributions, which correlates negatively with species trends (ρ_{with} = −0.319, *P* = 0.00792 and ρ_{without} = −0.457, *P* = 0.00208) and positively with the proportion of species distribution that is protected (ρ_{with} = 0.894 and ρ_{without} = 0.825, *P* < 0.001 for both) (Fig. 4a and b). Thus, a northerly distribution is more often associated with high proportion of protected distribution and a declining population trend. Similarly, southern species seem to be more often thriving, despite having the lowest coverage in protected areas and despite being identified as priority conservation targets in the gap analysis (Figs. 2a and 3).

The models built to project potential distributions under present and future climate showed good agreement between observed and modeled current distributions when using Cohen's Kappa statistic (K) (median and range values for ANN = 0.70, 0.19–0.99; CTA = 0.67, 0.27–0.98; GAM = 0.70, 0.34–0.99; and GLM = 0.71, 0.39–0.99), and excellent agreement when using the area under curve (AUC) of the receiver operating characteristic (Roc) curve (median and range values for ANN = 0.92, 0.56–0.99; CTA = 0.90, 0.69–0.99; GAM = 0.93, 0.82–1.0; and GLM = 0.93, 0.83–1.0). Based on the projections, most of the species of southern habitat types (deciduous forests, wetlands, and bushes and saplings) are expected to increase their distribution within protected areas, whereas species of the two northern habitats are expected to maintain or decrease their distributions (Fig. 2b). This implies that many of the species that are currently identified as gaps or partial gaps requiring further protection might go through a favorable

change in terms of coverage, given that the future range shifts follow the projected expectations. On the other hand, many of the currently well protected northern species will require further attention in the future due to the contracting potential distribution size. This projected outcome is congruent when compared with the current population trends in each of the habitat types (Fig. 2c).

There is also a positive correlation between the current population trends and the expected change in the overall distribution size in all of the four scenarios. This correlation is particularly strong among species with significant population trends (Spearman ρ_{without}: A1FI = 0.572; A2 = 0.570; B1 = 0.551; B2 = 0.546, *p*-values for all scenarios *P* < 0.001) but holds even if species with no observed trends (i.e. population trend index equals to zero) are included (Spearman ρ_{with}: A1FI = 0.406, *P* = 0.0014; A2 = 0.399, *P* = 0.0017; B1 = 0.388, *P* = 0.0024; B2 = 0.378, *P* = 0.0032, Fig. 4c, showing the results for the climate scenario A1FI). However, with the zero inflated data structure the correlation is naturally weaker. Correlation results imply that the species that currently have a declining population trend are also expected to experience a contraction of their climatic suitable ranges by the year 2050, whereas species with recent increases in population size are expected to experience an expansion.

4. Discussion

The comparison between population trends and the conservation priorities indicated by the gap analysis reveals a contradicting pattern: in terms of representation, the north is doing better than the south, but looking at population trends, the situation is the opposite. When expanding the time scale to include projected changes in species distributions under climate change, the difference becomes even more contrasting. As the poorly represented southern species will have increasing climatic suitability within protected areas, the well covered northern species, and especially species of arctic mountains, will very likely lose suitable climate
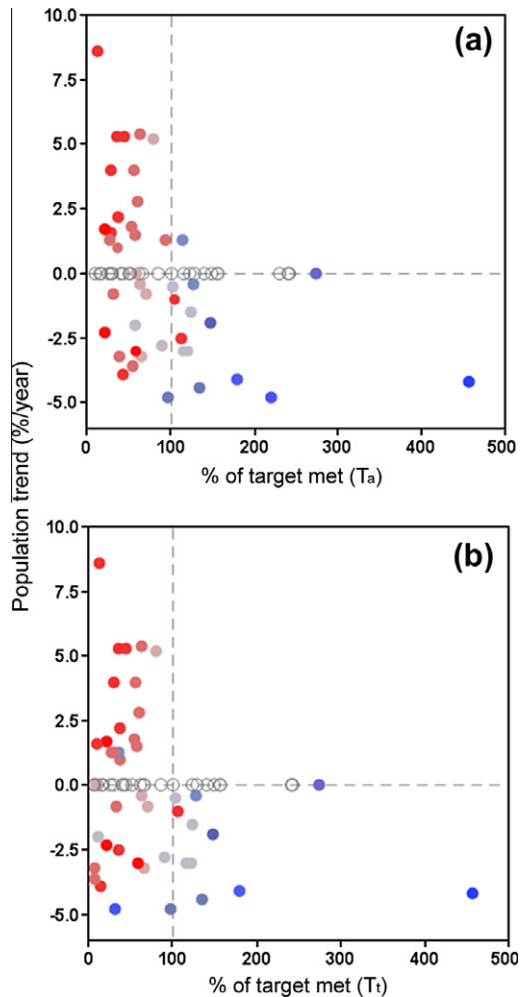
Fig. 3. Scatter plots showing the correlation between population trends and species coverage. Each dot presents one species, open circles are for species with no observed trend, colored circles for species with trends significantly different from zero. Plot (a) shows the correlation when targets have been assigned based on distribution size, and plot (b) when targets are based on threat categories. The color of the dots corresponds to the latitude of the weighted center of species' distributions showing the most southern species as red and the most northern species as blue.

within protected sites. Most importantly, the expected changes correlate positively with current population trends, implying that these changes might already be taking place. In the case of Finland, the results raise confusion on how conservation efforts should be allocated.

A standard interpretation of the gap analysis results obtained would support the view that greater conservation efforts are needed in the southern parts of the country. This interpretation would hold independent of the target setting scheme or the thresholds used for defining protected cells (Figs. 3 and A.3). This outcome can be explained by the polarized distribution of protected areas in Finland, with a concentration of large and uniform protected areas in North Finland, and only small and scattered reserves in the South (Fig. 1a). The Finnish protected area network is a classical example of how protected areas have not been carefully located in conservation priority sites in the past, but instead in remote, high altitude areas in lands of little economic value (Joppa and Pfaff, 2009). Earlier studies based on a subset of bird species and a subset of protected areas, and using transect surveys, have similarly found that the protected area network in Finland covers larger proportions of the total population size of northern

species in comparison to southern species (Virkkala and Raja-särkkä, 2007). Northern species have also been shown to have had more positive population trends inside than outside the protected areas at least up until 1980s (Virkkala, 1991). The poor representation levels of southern species associated with lush and deciduous forests, bushes and wetlands can be further explained by the fact that the majority of the small and scattered southern reserves are mostly on pine-dominated areas (Virkkala et al., 1994). All in all, the nationwide gap analysis seems to give very similar results to previous studies done with population density surveys inside and outside protected areas at smaller scales. The results also strongly support the recent conservation strategies in Finland, which have aimed at increasing the coverage and connectedness of protected areas in southern Finland (e.g. Kaakkinen et al., 2008).

On the other hand, we have shown that the population trends of common species decline when moving from South to North. The mismatch between gaps and population trends correlates with latitude and with the projected change in the climatic suitability for species, suggesting that one of the driving factors behind such mismatch could be ongoing climate change. Because abundance is known to correlate with range size (Gaston et al., 1997), the leading and trailing edges of species distributions would likely experience changes in population densities before actual range shifts (e.g. Parmesan and Yohe, 2003; Shoo et al., 2005). In this study, this process is evident among those species for which Finland constitutes the northernmost and southernmost extent. This could alter our perception of where our conservation priorities are: northern species are likely to eventually contract their ranges and possibly disappear from Finland entirely (Virkkala et al., 2008), despite conservation efforts aimed at protecting their existing habitat. Concurrently, it is expected that many southern species will expand their distributions northwards, gaining better coverage in protected areas. Although recorded population trends are likely driven by several interacting factors, the clear correlation with latitude and projected changes in distributions supports the proposition that ongoing changes in climate might be involved in governing recent population trends. Similar patterns have been detected in other parts of Europe, where especially after the mid-1980s climate has become an important driver of bird population trends (Gregory et al., 2009; Julliard et al., 2004).

Certain aspects need to be kept in mind when interpreting our results. First, alternative explanations of why population trends correlate negatively with representation in protected areas can be found for species of particular habitat types. For example, the declining population trends of species of open peatlands could be explained by the massive drainage and modification of mires in Southern Finland. The rate of drainage was most rapid from 1950s to 1970s, but has continued also from 1980s to present day, though less steeply (Kaakkinen et al., 2008). Thus, even though species of open peatlands are well represented in the current protected areas, the notable loss of habitat outside protected areas could result in overall decline of the entire population. However, analogous explanations for other habitat groups are not easily found. In particular, based on the national forestry statistics, there has been no significant change in the forest composition, age structure or in the amount of dead wood in the past 30 years that could explain the strongly positive population trends of species associated with deciduous or old-growth forest habitats (Peltola, 2008). It is important to remember that the population trend data describe the status of relatively common species, and therefore reflect changes taking place at a large scale and within fairly large populations.

Second, it is well known that forecasting future events is coupled with uncertainty. For example, species distribution models forecasting expected responses to climate change have been criticized for underestimating the role of certain biological processes,
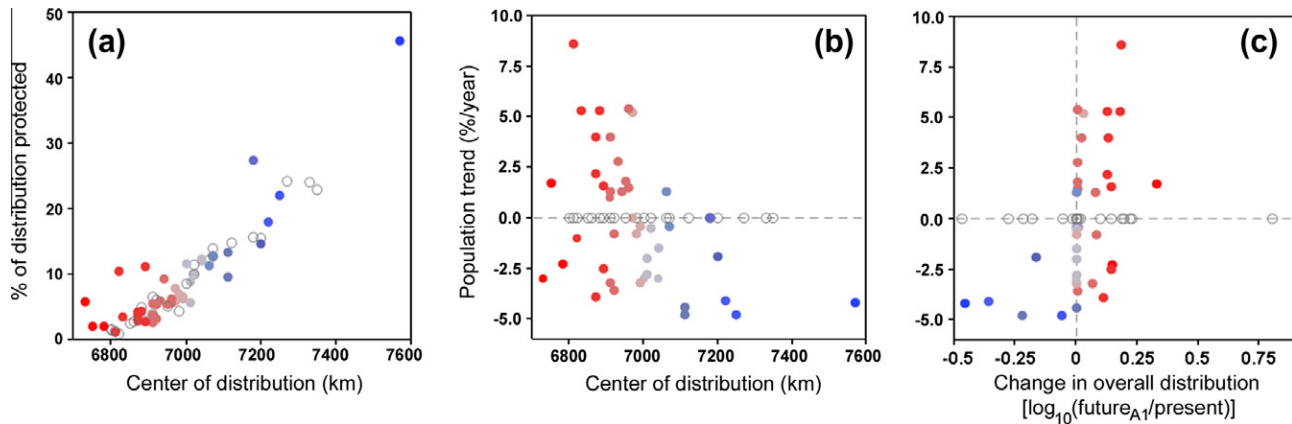
Fig. 4. Scatter plots showing the correlations between species coverage, population trends, latitude and projected distribution changes. Each dot presents one species, open circles are for species with no observed trend, colored circles for species with trends significantly different from zero. Plots (a) and (b) show how the level of protection and the population trend changes along latitude (measured as kilometers north from the equator). Plot (c) shows the correlation between population trends and the projected changes in the overall distribution size in Finland, measured as the logarithm ($\log_{10}$) of the proportion of grid cells occupied in the year 2050 under the emission scenario A1FI over the number of grid cells presently occupied. The color of the dots corresponds to the latitude of the weighted center of species' distributions showing the most southern species as red and the most northern species as blue.

such as species dispersal and complex interspecific interactions (e.g. Davis et al., 1998; Hampe, 2004) and for being sensitive to the choice of the modeling technique, climate model and emission scenario (e.g. Buisson et al., 2010). For discussion about uncertainties in species distribution modeling see e.g. Guisan and Thuiller (2005), Heikkinen et al. (2006) and Dawson et al. (2011). Nonetheless, by testing species distribution models in hind casting exercises, it has been shown that they can provide adequate results (Pearman et al., 2008), corresponding well to past population trends (e.g. Gregory et al., 2009). In studies with plants and mammals, they have been proven to be as powerful as mechanistic models (e.g. Kearney et al., 2010; Morin and Thuiller, 2009). In this study we have tried to decrease the amount of uncertainty by using ensemble modeling strategy where 75% or more of the models need to agree for a grid cell to be considered climatically suitable for a species. Also, we have tried to keep our interpretations conservative by looking only at large scale changes in the suitable climate, avoiding to make clear cut assumptions about changes in range, abundance or extinction risks. We have also focused on fairly common species that are less likely to suffer extensively from other anthropogenic pressures such as habitat loss or hunting. It is important to be cautious when interpreting modeling results and conclusions of policy relevance. However, as uncertain as future processes are, species range shifts are already being documented in nature at accelerating rate (e.g. Devictor et al., 2008; Hickling et al., 2006; Zuckerberg et al., 2009), and it is becoming more evident that climate change poses unprecedented challenges to conservation planning (e.g. Hannah et al., 2007).

While the observation that gap analysis based on current distributions does not capture future changes is unsurprising, the mismatch between population trends and the conservation gaps raises questions about the adequacy of simple implementations of this approach as a decision support tool for conservation planning. Although the ability of gap analyses to account for the mechanisms affecting long-term persistence of species has been debated (e.g. Jennings, 2000; Margules and Pressey, 2000; Rodrigues et al., 2004b), to our knowledge this is the first study demonstrating that gap analysis results imply different conservation priorities than indicators of current persistence (i.e. population trends). This is troublesome, resulting in mixed guidance on where and for which species current conservation actions are needed.

With this study we thus warn about the risks of using over simplistic implementations of gap analyses based on only current dis-

tribution data, even for short term assessments. The findings of this and other recent studies (e.g. Dockerty et al., 2003; Hannah et al., 2007) suggest the need for going beyond current observed distribution patterns when identifying priorities in conservation, especially in high latitudes and altitudes where climate change is expected to become the main threat to biodiversity in the future, rapidly re-shaping species distribution patterns (Jetz et al., 2007). This, however, does not mean that present day threats and priorities should be ignored: Habitat loss poses and will continue to pose a significant threat to species, especially in tropical regions. Also, evaluation of gap analysis results should not be restricted to the methods and data sets used in this study. Many other data sources such as threat assessments and changes therein, museum collections, development scenarios etc. can provide useful insights. We thus urge the use of additional information on species status and trends whenever possible, together with assessments of current priorities against projections of climate or land use driven distribution changes, when performing gap analyses.

Appendix A. Supplementary material and Appendix B. List of species and their attributes

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.06.023.

References

Araújo, M.B., 2004. Matching species with reserves – uncertainties from using data at different resolutions. Biol. Conser. 118, 533–538.

Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22, 42–47.

Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species–climate impact models under climate change. Glob. Change Biol. 11, 1504–1513.

Araújo, M.B., Thuiller, W., Pearson, R.G., 2006. Climate warming and the decline of amphibians and reptiles in Europe. J. Biogeo. 33, 1712–1728.

Buisson, L., Thuiller, W., Casajus, N., Lek, S., Grenouillet, G., 2010. Uncertainty in ensemble forecasting of species distribution. Glob. Change Biol. 16, 1145–1157.

Cabeza, M., Moilanen, A., 2001. Design of reserve networks and the persistence of biodiversity. Trends Ecol. Evol. 16, 242–248.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., Wood, S., 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391, 783–786.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond predictions: biodiversity conservation in a changing climate. Science 332, 53–58.

Devictor, V., Julliard, R., Couvet, D., Jiguet, F., 2008. Birds are tracking climate warming, but not fast enough. Proc. Roy. Soc. B: Biol. Sci. 275, 2743–2748.

Diniz-Filho, J.A.F., Mauricio Bini, L., Fernando Rangel, T., Loyola, R.D., Hof, C., Nogués-Bravo, D., Araújo, M.B., 2009. Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. Ecography 32, 897–906.

Dockerty, T., Lovett, A., Watkinson, A., 2003. Climate change and nature reserves: examining the potential impacts, with examples from Great Britain. Glob. Environ. Change 13, 125–135.

Donald, P.F., Sanderson, F.J., Burfield, I.J., Bierman, S.M., Gregory, R.D., Waliczky, Z., 2007. International conservation policy delivers benefits for birds in Europe. Science 317, 810–813.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.

GAP, 2010. <http://gapanalysis.nbii.gov/> (Retrieved 03.06.10).

Gaston, K.J., Blackburn, T.M., Lawton, J.H., 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. J. Anim. Ecol. 66, 579–601.

Gregory, R.D., Willis, S.G., Jiguet, F., Voříšek, P., Klvaňová, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D., Green, R.E., 2009. An indicator of the impact of climatic change on european bird populations. PLoS ONE 4, e4678.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Gurd, D.B., Nudds, T.D., Rivard, D.H., 2001. Conservation of mammals in eastern North American wildlife reserves: how small is too small? Conserv. Biol. 15, 1355–1363.

Hagemeijer, W.J.M., Blair, M.J., 1997. The EBCC Atlas of European Breeding Birds, Their Distribution and Abundance. Poyser, London.

Hampe, A., 2004. Bioclimate envelope models: what they detect and what they hide. Glob. Ecol. Biogeo. 13, 469–471.

Hannah, L., Midgley, G.F., Andelman, S., Araújo, M.B., Hughes, G., Martinez-Meyer, E., Pearson, R.G., Williams, P.H., 2007. Protected area needs in a changing climate. Front. Ecol. Environ. 5, 131–138.

Hario, M., Rintala, J., 2007. Tiirojen, sotkien, naurulokin ja haahkan kannankehitys rannikoilla 1986–2006. In: Lehtiniemi, T., Alanko, S. (Eds.), Linnut-vuosikirja 2006 (The yearbook 2006 of the Linnut magazine). Suomen Graafiset Palvelut, Kuopio, pp. 36–42.

Hario, M., Rintala, J., 2008. Haahkan ja lokkien kannakehitys rannikoilla 2005–2006. In: Solonen, T., Alanko, S. (Eds.), Linnut-vuosikirja 2007 (The yearbook 2007 of the Linnut magazine). Suomen Graafiset Palvelut, Kuopio, pp. 52–59.

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W., Sykes, M.T., 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progr. Phys. Geo. 30, 751–777.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Glob. Change Biol. 12, 450–455.

Hulbert, A.H., Jetz, W., 2007. Species richness, hotspots, and the scale dependence or range maps in ecology and conservation. Proc. Nat. Acad. Sci. USA 104, 13384–13389.

Hyytiä, K., Kellomäki, E., Koistinen, J. (Eds.), 1983. Suomen lintuatlas (The Finnish bird atlas). SLY:n Lintutieto Oy, Helsinki.

IPCC, 2007. Climate change 2007: synthesis report. In: Core Writing Team, Pachauri, R.K., Reisinger, A., (Eds.), Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

IUCN, UNEP, 2005. The World Database on Protected Areas (WDPA). UNEP-WCMC, Cambridge, UK.

Jennings, M.D., 2000. Gap analysis: concepts, methods, and recent results. Landsc. Ecol. 15, 5–20.

Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biol. 5, e157.

Joppa, L.N., Pfaff, A., 2009. High and far: biases in the location of protected areas. PLoS ONE 4, e8273.

Julliard, R., Jiguet, F., Couvet, D., 2004. Common birds facing global changes: what makes a species at risk? Glob. Change Biol. 10, 148–154.

Kaakkinen, E., Kokko, A., Aapala, K., Kalpio, S., Eurola, S., Haapalehto, T., Heikkilä, R., Hotanen, J.-P., Kondelin, H., Nousiainen, H., Ruuhijärvi, R., Salminen, P., Tuominen, S., Vasander, H., Virtanen, K., 2008. Mires. In: Raunio, A., Schulman, A., Kontula, T. (Eds.), Assessment of Threatened Habitats in Finland

– Part I: Results and Basis for Assessment. Suomen ympäristö 8/2008, Finnish Environment Institute, Helsinki, pp. 75–109.

Kearney, M.R., Wintle, B.A., Porter, W.P., 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conserv. Lett. 3, 203–213.

Langhammer, P.F., Bakarr, M.I., Bennun, L.A., Brooks, T.M., Clay, R.P., Darwall, W., De Silva, N., Edgar, G.J., Eken, G., Fishpool, L.D.C., da Fonseca, G.A.B., Foster, M.N., Knox, D.H., Matiku, P., Radford, E.A., Rodrigues, A.S.L., Salaman, P., Sechrest, W., Tordoff, A.W., 2007. Identification and Gap Analysis of Key Biodiversity Areas: Targets for Comprehensive Protected Area Systems. IUCN, Gland, Switzerland.

Liu, C., White, M., Newell, G., 2011. Measuring and comparing the accuracy of species distribution models with presence–absence data. Ecography doi:10.1111/j.1600-0587.2010.06354.x.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M., New, M., 2003. A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1990–2000) and 16 scenarios (2001–2100). In: Tyndall Centre Working Paper, Report No. 55. Tyndall Centre.

Morin, X., Thuiller, W., 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology 90, 1301–1313.

Nakicenovic, N., Swart, R. (Eds.), 2000. Special Report on Emissions Scenarios. Cambridge University Press, Cambridge, UK.

New, M., Lister, D., Hulme, M., Makin, I., 2002. A high-resolution data set of surface climate over global land areas. Climate Res. 21, 1–25.

O'Grady, J.J., Reed, D.H., Brook, B.W., Frankham, R., 2004. What are the best correlates of predicted extinction risk? Biol. Conserv. 118, 513–520.

Pannekoek, J., van Strien, A., 2004. TRIM 3 Manual (TRends & Indices for Monitoring data). Statistics Netherland, Voorburg.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Pearman, P.B., Randin, C.F., Broennimann, O., Vittoz, P., Knaap, W.O.v.d., Engler, R., Lay, G.L., Zimmermann, N.E., Guisan, A., 2008. Prediction of plant species distributions across six millennia. Ecol. Lett. 11, 357–369.

Peltola, A., 2008. Finnish Statistical Yearbook of Forestry. SVT Agriculture, forestry and fishery 2008, Finnish Forest Research Institute, Vammala.

Rassi, P., Alanen, A., Kanerva, T., Mannerkoski, I., 2001. Suomen lajien uhanalaisuus 2000 (The Red List of Finnish Species). Ministry of the Environment & Finnish Environmental Institute, Helsinki.

Rodrigues, A.S.L., Akcakaya, H.R., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Chanson, J.S., Fishpool, L.D.C., Da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004a. Global gap analysis: priority regions for expanding the global protected-area network. BioScience 54, 1092–1100.

Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004b. Effectiveness of the global protected area network in representing species diversity. Nature 428, 640–643.

Rondinini, C., Wilson, K.A., Boitani, L., Grantham, H., Possingham, H.P., 2006. Tradeoffs of different types of species occurrence data for use in systematic conservation planning. Ecol. Lett. 9, 1136–1145.

Scott, J.M., Csuti, B., Jacobi, J.J., Estes, J.E., 1987. Species richness: a geographic approach to protecting future biological diversity. BioScience 37, 782–788.

Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., Derchia, F., Edwards, T.C., Ulliman, J., Wright, R.G., 1993. Gap analysis – a geographic approach to protection of biological diversity. Wildl. Mono., 1–41.

Shoo, L.P., Williams, S.E., Hero, J.-M., 2005. Potential decoupling of trends in distribution area and population size of species with climate change. Glob. Change Biol. 11, 1469–1476.

Sowa, S.P., Annis, G., Morey, M.E., Diamond, D.D., 2007. A gap analysis and comprehensive conservation strategy for riverine ecosystems of Missouri. Ecol. Mono. 77, 301–334.

Tear, T.H., Scott, J.M., Hayward, P.H., Griffith, B., 1993. Status and prospects for success of the endangered species act: a look at recovery plans. Science 262, 976–977.

Thuiller, W., Brotons, L., Araújo, M.B., Lavorel, S., 2004. Effects of restricting environmental range of data to project current and future species distributions. Ecography 27, 165–172.

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. PNAS 102, 8245–8250.

Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32, 369–373.

Tucker, G.M., Heath, M.F., 1994. Birds in Europe: Their Conservation Status. BirdLife International (Conservation Series No. 3), Cambridge, United Kingdom.

Väisänen, R.A., 2005. Suomen pesivän maalinnuston 84 lajin kannanvaihtelut 1983-2004. In: Yrjölä, R., Nikander, P.J. (Eds.), Linnut-vuosikirja 2004 (The Yearbook 2004 of the Linnut Magazine). Suomen Graafiset Palvelut, Kuopio, pp. 105–119.

Väisänen, R.A., 2006. Maalinnuston kannanvaihtelut Etelä-ja Pohjois-Suomessa 1983-2005. In: Yrjölä, R., Alanko, S. (Eds.), Linnut-vuosikirja 2005 (The Yearbook 2005 of the Linnut Magazine). Suomen Graafiset Palvelut, Kuopio, pp. 83–98.

Väisänen, R.A., Lammi, E., Koskimies, P., 1998. Muuttuva pesimälinnusto. Otava, Keuruu.

Virkkala, R., 1991. Population trends of forest birds in a Finnish Lapland landscape of large habitat blocks: Consequences of stochastic environmental variation or regional habitat alteration? Biol. Conserv. 56, 223–240.

Virkkala, R., Rajasärkkä, A., 2007. Uneven regional distribution of protected areas in Finland: consequences for boreal forest bird populations. Biol. Conserv. 134, 361–371.

Virkkala, R., Rajasärkkä, A., Väisänen, R.A., Vickholm, M., Virolainen, E., 1994. The significance of protected areas for the land birds of Southern Finland. Conserv. Biol. 8, 532–544.

Virkkala, R., Heikkinen, R.K., Leikola, N., Luoto, M., 2008. Projected large-scale range reductions of northern-boreal land bird species due to climate change. Biol. Conserv. 141, 1343–1353.

Zuckerberg, B., Woods, A.M., Porter, W.F., 2009. Poleward shifts in breeding bird distributions in New York State. Glob. Change Biol. 15, 1866–1883.