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Does the protected area network preserve bird species of conservation concern in a rapidly changing climate?

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26 **Abstract**

27

28 Species ranges are expected to move polewards following the changing climate, which poses novel
29 challenges to the protected area network, particularly at northern latitudes. Here we study how well
30 protected areas are likely to sustain populations of birds of conservation concern under a changing
31 climate in northern Europe, in Finland. We fitted bioclimatic envelope models generated for 100
32 bird species to climate scenario data for the years 2051–2080 and three alternative emission
33 scenarios in a 10-km grid system to predict changes in the species probability of occurrence. We
34 related the projected changes in the climatic suitability to the amount of protected preferred habitat
35 for the study species in the 10-km grid cells, and based on the cover of four main CORINE Land
36 Cover classes in each conservation area in Finland. The probability of occurrence of all species
37 (except marshland birds) decreased according to all scenarios, the decline being greatest in southern
38 and smallest in northern boreal zones. This decline was slightly greater in unprotected than in
39 protected areas for species of forests, mires and mountain habitats. The climatically suitable areas
40 for the species were predicted to shift northwards, but the potential gain of southern species of
41 conservation concern appears not to compensate for the loss of northern species. Thus, a
42 representative protected area network is needed in all boreal zones. Overall, our results show that
43 species-specific habitat preferences and habitat availability should be taken into account when
44 assessing the efficiency of a protected area network in a changing climate.

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46

47 **Keywords:** climate change, habitat availability, protected area network, range shift, species of
48 conservation concern

49 **Introduction**

50

51 Global climate change is one of the key factors threatening biodiversity (Pereira et al. 2010), is
52 already affecting species populations and communities (Parmesan 2006; Chen et al. 2011), and is
53 projected to do so even more in the future (Beaumont and Hughes 2002; Thomas et al. 2004;
54 Thuiller et al. 2005a). One of the main instruments alleviating climate change impacts on
55 biodiversity are regional and national networks of protected areas. However, species ranges are
56 expected to move polewards following the changing climate (Parmesan 2006; Hitch and Leberg
57 2007; Huntley et al. 2007, 2008; Zuckerberg et al. 2009; Brommer et al. 2012), which poses novel
58 challenges to the protected area network, possibly decreasing their efficiency to preserve biota
59 (Araújo et al. 2004; Hannah and Salm 2005; Hannah et al. 2007). Under shifting species
60 distributions, reserve networks may cease to provide protection to those species for which they were
61 originally established (Coetzee et al. 2009; Hole et al. 2009; Araújo et al. 2011).

62

63 Loarie et al. (2009) compared the world's 14 main biomes and protected areas situated within them
64 and showed that climate residence time by 2100 was among the lowest in protected areas situated in
65 boreal forests. Moreover, climate change-driven range shifts are projected to be most dramatic at
66 northern latitudes because of the greater projected increases in temperature (Jetz et al. 2007). Given
67 these forecasts, the protected areas of boreal forests may face one of the greatest turnovers of biota
68 and one of the greatest decreases in climatic suitability for the species assemblages they currently
69 harbour. The importance of the assessments of the impacts of climate change on boreal biota and
70 reserve networks is accelerated due to the fact that landscapes and environments in northern Europe
71 are also affected by man's direct land use, such as intensive forest management, drainage of mires,
72 intensified agriculture, and ultimately, fragmentation of a previously uniform forest landscape
73 (Virkkala and Toivonen 1999). As a consequence, many species are threatened by certain types of

land use causing habitat loss (Rassi et al. 2010). Thus, the matrix areas between the nature reserves often provide only lower quality breeding sites for declined and threatened species, which makes the assessment of predicted changes in climatic suitability of protected areas for threatened species particularly important.

Some forecasts of the potential range shifts for the whole of Europe, or parts of it, are already available. Throughout Europe, bird species distributions have been projected to change considerably in the 21st century as a consequence of climate change (Huntley et al. 2007, 2008). Virkkala et al. (2008, 2010) showed that bird species particularly susceptible to the effects of climate warming are those with distributions concentrated in the northern boreal or Arctic zones, not least because the Arctic Ocean will effectively limit their range expansion northwards. These prospects are related to the severity of the climate change projections, which are stronger for northern Europe than in temperate and Mediterranean Europe (ACIA 2005). For example in Finland, mean annual temperature is expected to increase up to 7 °C by 2080 in comparison with the baseline period, 1961–1990 (Jylhä et al. 2004). Northward density shifts in populations of bird species in Finnish protected areas have already been observed with northern species showing greatest decrease in their trailing edge in southern Finland and southern species increasing most in their leading range boundary in northern Finland (Virkkala and Rajasärkkä 2011). Moreover, among species distributed over the whole country, there were population density shifts toward northern Finnish protected areas.

Bioclimatic envelope models (BEMs) are increasingly employed to assess the potential impacts of climate change on species distributions (Pearson and Dawson 2003; Guisan and Thuiller 2005; Heikkinen et al. 2006a; Garcia et al. 2011), based on the finding that on broad spatial scales, climatic variables are often good predictors of species distributions (Pearson and Dawson 2003;

99 Pearson et al. 2004; Thuiller 2004; Huntley et al. 2007; Triviño et al. 2011). Using BEMs, models
100 of the relationships between present-day distributions of species and current climatic variables can
101 be developed and then used to forecast the future changes in suitable climate space for species
102 under different climate scenarios (Thuiller et al. 2005b; Heikkinen et al. 2006a; Huntley et al. 2007,
103 2008; Virkkala et al. 2010). However, there are a number of potential shortcomings in many earlier
104 studies where BEMs have been applied to assess the impact of a changing climate on biota in a
105 reserve network. For example, they have converted the probability of occurrence data for present-
106 day and future conditions into plain presence/absence data based on a certain cut-off level, such as
107 prevalence (see Liu et al. 2005), and moreover, have employed only the total size of the
108 conservation areas (e.g. Araújo et al. 2011). They have very rarely investigated how much preferred
109 habitats or land cover types for the modelled species in the studied conservation areas actually exist.
110 The first shortcoming results in loss of information and potential lumping of drastic changes in
111 climatic suitability with marginal changes, and the latter runs the risk of making false assumptions
112 of the availability of protected habitat for a given species in a given locality (e.g. protected forests
113 rarely provide relevant habitats for marshland birds). Thirdly, very few studies, if any, have
114 examined how climatic suitability changes, specifically in the areas with largest amounts of suitable
115 protected habitat for the species of conservation concern (hereafter called "hotspots of protection").
116
117 In this paper we use bioclimatic envelope modelling to predict bird species probability of
118 occurrence to study how well-protected areas are likely to sustain biodiversity under a changing
119 climate in northern Europe. Using climate and species distribution data for present-day European
120 conditions, we calibrate BEMs for 100 bird species of conservation concern which are considered
121 based on several different classifications of bird species. The models are then applied to three
122 climate scenarios for the period 2051–2080 to estimate the changes in climatic suitability for these
123 100 species in the reserve network of Finland. We relate species predicted occurrences to the

amount of preferred habitat of each species. In other words, by applying the derived models to climate scenarios and comparing their projections with the present-day probability of occurrence values, we investigate the changes in the climatic suitability of nature conservation areas for the valuable bird species they currently hold. By using the European Bird Atlas (see Hagemeijer and Blair 1997) we were able to employ European-wide species distributions in the model calibrations. Hence species which presently do not breed in Finland, but occur to the south or south-east of Finland, were also included. Predicted range shifts of bird species of four natural habitats (forests, mires, marshlands, and Arctic mountain habitats) were studied in relation to the extent of these habitat types in protected areas. We (1) expect that changes in the probability of species occurrences are most pronounced in the northern boreal areas, because these regions face the largest climate changes and because northern species will probably be the most vulnerable to climate change; and (2) analyse whether changes in the projected climatic suitability are stronger or milder in protected areas compared with unprotected areas. We conjecture here that the stronger projected decline in suitability in protected than in unprotected areas indicates that the location of protected areas may be suboptimal in the future and the capacity of the network for maintaining rare bird species can deteriorate even more than expected from the mean changes in boreal landscapes.

Material and methods

Bird species

We studied distribution patterns of 100 land bird species of conservation concern, of which 51 was regarded as species of forests, 21 species of mires, 17 species of marshlands and 11 species of Arctic mountain habitats (Appendix 1). Of the species of mountain habitats, nine were regarded as

148 species of mountain heaths and two species (bluethroat *Luscinia svecica* and Arctic redpoll
 149 *Carduelis hornemanni*) of mountain birch (*Betula pubescens czerepanovii*) woods.

150

151 In addition to regularly breeding species (90 bird species) in Finland we also included species of
 152 conservation concern (eight forest species and two marshland species) that presently do not breed in
 153 Finland but are breeding in regions to the south of Finland (Baltic countries, Belarus) or south-east
 154 of Finland, in Russia (see Appendix 1). Thus, these species may possibly expand their ranges to
 155 Finland in the future. For example, southern marshland species the Savi's warbler *Locustella*
 156 *luscinioides*, the bearded parrotbill *Panurus biarmicus* and the penduline tit *Remiz pendulinus* have
 157 colonised Finland quite recently, during the past few decades (Valkama et al. 2011).

158

159 We selected the studied 100 species based on a number of conservation status classification lists.
 160 These classifications and the critical categories in them were the following (Appendix 1): the
 161 European Union's Birds Directive species (Annex I, special conservation actions needed, 46 species
 162 included), species of European conservation concern (unfavourable conservation status: SPEC1–
 163 SPEC3, 39 species; BirdLife International 2004a), species of Arctic or boreal biome in defining
 164 important bird areas in Europe (IBA) (Heath and Evans 2000; 24 species), threatened species in the
 165 European Union (unfavourable conservation status) (BirdLife International 2004b; 54 species),
 166 species of special responsibility in Finland (Rassi et al. 2001; 17 species), red-listed species in
 167 Finland in 2010 (near-threatened and threatened species) (Rassi et al. 2010; 43 species), and species
 168 preferring old-growth or mature forests in Finland (Virkkala et al. 1994; Väisänen et al. 1998;
 169 Virkkala and Rajasärkkä 2007; 16 species). A species was included in the study if it belonged to at
 170 least one of these classifications. Species of agricultural habitats or human settlements, and species
 171 of lakes (e.g. waterfowl) or the Baltic Sea were not included in the analysis because we

concentrated on terrestrial protected area network consisting of forests, mires and other wetlands (here regarded as marshlands) and mountain habitats.

Habitat classification and protection of habitats

Biogeographically, Finland stretches through the boreal coniferous vegetation zone. Therefore, habitats and protected areas were considered in three commonly used main vegetation zones from south to north: the southern boreal, the middle boreal and the northern boreal zone (cf. Virkkala and Toivonen 1999; Virkkala et al. 2000; see Fig. 1 and Fig. 2). The south-western coast of Finland belongs to the hemiboreal zone, but due to its small areal extent, it was included here in the larger southern boreal zone. Mountain birch forms the northernmost forests and constitutes the tree line in the mountains of northern boreal zone in northernmost Finland.

For broad-scale modelling of species distributions, the availability of systematically recorded land cover data over large areas is essential. We opted for CORINE Land Cover data here due to its complete spatial coverage in Finland, and because of the homogeneity of the methodology used for the land-cover classification at the pan-European level (EU countries). The classification of land cover into CORINE classes in Finland is based on automated interpretation of Landsat ETM satellite images with the resolution of 30 m and data integration with existing digital maps. Satellite image derived land cover data are combined with existing digital land use and soil information provided by the National Land Survey of Finland. The proportion of land cover types was calculated as a cover for each 10 x 10 km cell and within each of the conservation area included in the study from a digital CORINE database using ArcView Spatial Analyst (Version 3.2, ESRI, Redland, CA, USA).

197 CORINE Land Cover 2006 was used in defining the focal habitat types. Different coniferous,
 198 deciduous and mixed forest classes were combined as a single forest class except mountain birch
 199 woods above the coniferous forest boundary in the Arctic mountains in the northern boreal zone.
 200 Open mires (i.e. treeless peatlands) were regarded as mire class. Following Virkkala et al. (2005),
 201 wetlands (excluding mires) mostly along sea and lake shores and along rivers and in estuaries were
 202 regarded as marshland habitats. Thus, these type of marshlands are specific wetlands largely
 203 dominated by the common reed *Phragmites australis* in Europe. Open, treeless Arctic mountain
 204 areas situated in the northern boreal zone were included as mountain heaths. The total land area of
 205 forests was 184,854 km² (60.7% of total land area of 304,474 km² in Finland), open mires 35,761
 206 km² (11.7%), marshlands 963 km² (0.3%), mountain heaths 7,368 km² (2.4%) and mountain birch
 207 woods 3,138 km² (1.0%).

208
 209 Protected habitat obtained consisted of strictly protected areas in which economic use of habitats,
 210 such as logging or drainage of wetlands, is not allowed. We included protected areas (national
 211 parks, strict nature reserves, mire conservation areas, bird wetland areas, old-growth forest areas,
 212 herb-rich forest areas, other protected areas on state-owned or privately owned land and wilderness
 213 areas) and officially accepted protection programmes of specific habitats (old-growth forests, herb-
 214 rich forests, mires and bird wetland areas), which consisted partly of areas not yet legally protected
 215 but to be founded as protected areas in the near future. All Natura 2000 areas, which are
 216 implemented by nature conservation act (e.g. logging is not allowed) are included in our analysis.

217
 218 The amount of protected habitat differs considerably both from south to north and between-habitat
 219 types (Appendix 2, Fig. 1). There are large (over 1000 km² in size) national parks, wilderness areas
 220 and other protected areas in northernmost Finland. According to the CORINE Land Cover
 221 classification and digitized protected areas, 2.3% of forests in the southern boreal zone, 3.7% in the

222 middle boreal zone and 23.4% in the northern boreal zone were included in protected areas.
 223 Corresponding figures of the proportion protected for mires were 19.0%, 19.4% and 35.2%, and for
 224 marshlands 26.7%, 24.2% and 12.1%, respectively. In Arctic mountain heaths 88.9% and in
 225 mountain birch woods 82.4% were situated in protected areas.
 226
 227 For the purposes of this study, the focal "protected" squares were interpreted as the top 5% of 10 x
 228 10 km grid cells with the highest amount of protected habitat type, measured separately for each
 229 vegetation zone and each habitat type. The number of these 5% "hotspots" of protected squares
 230 were 79 (total no. of squares = 1582), 58 (total = 1165) and 54 (total = 1077) in the southern boreal,
 231 middle boreal and northern boreal zones, respectively. The location of these hotspot squares also
 232 varied among the habitat types (Fig. 2). The hotspot squares for forests consisted of 44.5%, 44.3%
 233 and 28.8% of all protected forests in the southern, middle and northern boreal zones, respectively.
 234 The corresponding figures for protected mires were 68.5%, 47.8% and 30.1% and for marshlands
 235 69.9%, 77.7% and 79.3% of their protected habitats in each zone. In mountain heaths 56.1% and in
 236 mountain birch woods 52.5% of the protected habitats were situated in the 5% hotspot squares
 237 (Appendix 2).
 238
 239 We used "unprotected" squares (10-km grid squares with only few or no protected areas) for each
 240 habitat type as a comparison point. These were selected otherwise randomly in each zone but using
 241 a criteria that the lowest amount of protected habitat in the 5%-hotspot-protected-squares was
 242 regarded as the minimum amount of unprotected habitat for the unprotected squares to be selected.
 243 An equal number of unprotected squares and protected squares were selected in each zone. Because
 244 over 80% of the mountain heaths and mountain birch woods were situated in protected areas,
 245 unprotected squares in these habitat types were selected to have the least amount of protected
 246 mountain habitat within unprotected squares (see Appendix 2).

247

248 Each bird species was related to its main habitat in Finland or areas south of Finland (Appendix 1).

249 Therefore, species such as the temminck's stint *Calidris temminckii* or the common ringed plover

250 *Charadrius hiaticula*, for example, were regarded as species of Arctic mountain heaths, as the vast

251 majority of breeding populations occurs there (see Väisänen et al. 1998), although these species

252 sometimes occur in other habitats, too. In our analyses of changes in the probability of occurrence,

253 species of Arctic mountain heaths and birch woods were combined as Arctic mountain species.

254

255 Atlas data

256

257 We used the European Bird Atlas (Hagemeijer and Blair 1997) in developing the bioclimatic

258 envelope models for the studied 100 bird species. The European Bird Atlas uses 50 km grid cell,

259 and we used present-absent data from all the squares where data covered at least 75% of expected

260 breeding species (2300 squares, see Hagemeijer and Blair 1997). Following Huntley et al. (2007),

261 other observed records in poorly studied squares (data covered less than 75% of expected species)

262 were included as complementary known occurrences of species, by adding them to the data on well-

263 surveyed grid cells on a species-by-species basis (resulting in slight differences in the total number

264 of grid cells used in the modelling of individual bird species, the total number of grid cells varying

265 from 2303 to 2622 between the individual species). This complementary data came mostly from

266 Russia, Ukraine, Belarus and Romania. A species was considered as breeding in a grid cell when

267 the record for it fell under one of these categories: possible, probable and confirmed breeding.

268 Almost all of original atlas field work was carried out in the different European countries between

269 1976 and 1995.

270

271 Climate data and scenarios

272

273 Based on the knowledge on the main climatic drivers of the bird species distributions in Europe
 274 (Huntley et al. 2007) and especially in northern European environments (Forsman and Mönkkönen
 275 2003; Heikkinen et al. 2006b; Virkkala et al. 2008), we selected five climate variables as potential
 276 explanatory variables for BEMs: mean temperature in April–June ($TEMP_{AMJ}$), mean temperature of
 277 the coldest month (MTCO), annual daily temperature sum above 5°C (growing degree days,
 278 GDD5), mean precipitation in April–June ($PREC_{AMJ}$), and mean annual precipitation (PREC).

279

280 Because a data set in a 10' –grid scale for the period 1971–2000 was not readily available, an
 281 observed climate dataset of monthly mean temperature and precipitation in 10' x 10' spatial
 282 resolution averaged for the period 1971–2000 was constructed by combining two gridded databases:
 283 the CRU_TS_3.1 data set in 30' x 30' grid resolution with monthly data for each year during the
 284 period 1961–2000 (updated from Mitchell and Jones (2005)), and monthly climatologies for the
 285 period 1961–1990 in 10' x 10' grid resolution from the CRU_CL_2.0 data set (New et al. 2002).
 286 Absolute monthly differences (deltas) between the periods 1971–2000 and 1961–1990 have been
 287 calculated from CRU TS 3.1 and bi-linearly interpolated to the higher 10'-spatial resolution. The
 288 deltas were then added to the 1961–1990 climatology in 10' resolution. Data have been extracted
 289 for Eurasia defined as the land grid cells for the window 12°W to 70°E longitude and 34°N to 72°N
 290 latitude consisting of 73670 grid cells in 10' resolution and 9167 grid cells in 30' resolution.

291

292 We estimated growing degree days by interpolating monthly mean temperature to daily values
 293 using a sine-curve interpolation. Growing degree days was then calculated as the daily sum of
 294 temperature above 5°C accumulated over the whole year.

295

Observed climate data in 10' resolution were matched to the 50 x 50 km grid system used in the European Bird Atlas data by calculating three different values for mean temperature in April–June, mean temperature of the coldest month and growing degree days to indicate the regional variation in these climate parameters in the 50 x 50 km cells. We calculated the mean, minimum and maximum temperature among 10' grid cells whose centre point was located within a given 50 x 50 km cell. The minimum and maximum values were included so that our BEMs would be better equipped to capture the preferences of bird species favouring lowland or upland climate conditions, which might have been lost in the mean values calculated for the 50 x 50 km cells. Overall, 11 individual climate variables were considered in the model building, nine of which represented the mean, maximum and minimum of single variables (Appendix 3). Mean precipitation in April–June and mean annual precipitation were included in the modelling only as the mean value of the 10' cells embedded within a 50- km cell, because the variation of precipitation within the 50-km cells was lower than that of temperature.

Three climate scenarios representing the range of possible period-mean conditions for 2051–2080 were constructed for the above climate variables on a 10 x 10 km grid covering Finland. Temperature and precipitation data for an ensemble of 19 General Circulation Models employed in the IPCC's Fourth Assessment Report (IPCC 2007) (General Circulation Models: BCCR-BCM2.0, CGCM3.1/T47, CGCM3.1/T63, CNRM-CM3, CSIRO-MK3.0, GFDL-CM2.0, GFDL-CM2.1, GISS-ER, INM-CM3.0, IPSL-CM4, MIROC3.2/hires, MIROC3.2/medres, ECHO-G, ECHAM5/MPI-OM, MRI-CGCM2.3.2, NCAR-CCSM3, NCAR-PCM, UKMO-HadCM3, UKMO-HadGEM1) were downloaded from the archive of the Third Coupled Model Intercomparison Project (CMIP3; Meehl et al. 2007). One central ensemble scenario and two single GCM simulations representing low and high changes were selected. These were: (i) the 19-model ensemble average for the SRES A1B emission scenario representing average changes; (ii) a

simulation of the Australian CSIRO-MK3.0 GCM for the SRES B1 (from now on B1) scenario, which consistently gives relatively low annual temperature and precipitation changes over Finland throughout the 21st century; and (iii) a simulation of the Japanese MIROC3.2/medres GCM for the SRES A2 (from now on A2) scenario which consistently ranks among those simulations giving higher annual temperature and precipitation increases for Finland.

Statistical analyses

The European climate and bird data were employed to calibrate the bioclimatic models for each study species separately. Because the mean, maximum and minimum values for TMP_{AMJ} , MTCO and GGD5 were highly intercorrelated, we ran a pilot analysis using generalized additive models (GAM) via the GRASP user-interface in S-PLUS (Lehmann et al. 2003) to select either mean, maximum or minimum of each of these variables into the actual modelling. Here we scrutinised the variable alone (the variable on its own, i.e. in a univariate model), the drop contribution (i.e. when the variable is dropped from the full model) and the model contribution (i.e. the contribution of each predictor within the selected models) indicating the relative importance of a predictor variable provided by GRASP. The mean, maximum or minimum value showing the highest importance (i.e. ranking highest in two or three of the criteria employed: univariate, drop and model contribution) was selected to present TMP_{AMJ} , MTCO and GGD5 for each species separately. In the few cases where the mean, maximum and minimum all ranked highest in one of the criteria, the climate variable with the highest alone contribution was selected. Next, a second GRASP run was performed including the remaining five climate variables, and then in cases where high (>0.9) correlations between the five predictor variables appeared, a variable with lower importance in alone, drop and model contributions were excluded. As a result of this selection procedure, different temperature variables were often selected for different species (see Appendix 3). However, for the

346 precipitation variables we used only the mean values of the 10' x 10' grid cells, and because their
347 correlation with the other variables was always below <0.8 (cf. Denoel and Ficetola 2008) we
348 included these two variables in all our BEMs.

349

350 The bioclimatic envelope models calibrated with the European climate (1971–2000) and bird data at
351 the 50 x 50 km resolution were first fitted to the climate data for Finland averaged over the period
352 1971–2000 in the 10 x 10 km grid system. This provided the baseline estimate of the climatic
353 suitability (i.e., predicted probability of occurrence) of each 10 x 10 km grid cell for each bird
354 species, with the focus on the grid cells having the highest amount of suitable protected habitat for a
355 given species and the unprotected grid cells used in comparisons. Next, we fitted the derived
356 models to the three climate scenario data sets for the time period 2051–2080 which provided
357 estimates of the future climatic suitability for each species in the same 10-km grid cells. By
358 comparing the predicted climatic suitability in 1971–2000 to those in 2051–2080 we generated an
359 estimate of the change in the climatic suitability.

360

361 The bioclimatic envelope models were generated using the BIOMOD framework (the version
362 described in Thuiller et al. 2009) in the R environment version 2.12.2 , and the three modelling
363 techniques embedded in BIOMOD, namely generalized linear models (GLM), generalized additive
364 models (GAM) and generalized boosting method (GBM), which have performed well in
365 extrapolative modelling (Heikkinen et al. 2012; see also Austin et al. (2006); Elith et al. (2006);
366 Duncan et al. (2009)). For each of the 100 bird species, polynomial GLMs were computed using an
367 automatic forward stepwise procedure together with the Akaike information criterion (AIC) model
368 selection criteria (Thuiller et al. 2009). Generalized additive models (GAM) (Hastie and Tibshirani
369 1990) are nonparametric extensions of GLM, which provide a flexible, data-driven class that
370 permits both linear and complex additive response shapes. A cubic-spline smoother with three

degrees of freedom, and the step forward variable selection of GAM in BIOMOD based on AIC were employed (Thuiller 2003). The generalized boosting method (GBM) is highly efficient in fitting the data, it is nonparametric and combines the strengths of different modern statistical techniques (Ridgeway 1999). GBM was implemented into R (R Development Core Team, 2004) using the library GBM (Generalized Boosted Regression Modelling). The maximum number of trees was set to 2,000, and a four-fold cross-validation procedure was performed. For more details of these three modelling methods, see McCullagh and Nelder (1989), Lehmann et al. (2003), Austin et al. (2006), Elith et al. (2006, 2008), and Marmion et al. (2009).

We examined the predictive power of the derived models using a four-fold cross validation with random split into 20% validation and 80% calibration data sets, and assessed the discrimination ability of the predictive models using three different measures: 1) the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding and Bell 1997), 2) the kappa statistic (Congalton 1991), and 3) true skill statistic (TSS; Allouche et al. (2006)). AUC relates relative proportions of correctly classified (true positive proportion) and incorrectly classified (false positive proportion) cells over a wide and continuous range of threshold levels, which makes it a threshold-independent measure (Pearce and Ferrier 2000). An approximate guide for classifying the accuracy of models using AUC is (Swets 1988): 0.90–1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; 0.50–0.60 = fail. The kappa coefficient measures the correct classification rate (proportion of correctly classified presences and absences) after the probability of chance agreement has been removed (Congalton 1991). Landis and Koch (1977) proposed a scale to describe the degree of concordance: 0.81–1.00 = almost perfect, 0.61–0.80 = substantial, 0.41–0.60 = moderate, 0.21–0.40 = fair, 0.00–0.20 = fail. TSS is measured as: sensitivity + specificity – 1, where sensitivity is the proportion of correctly predicted presences and specificity the proportion of correctly predicted absences. TSS is independent of prevalence (see Allouche et al. 2006). For the

396 TSS, values from 0.2 to 0.5 can be regarded as poor, values from 0.5–0.8 as useful, and values
 397 larger than 0.8 as excellent (Coetzee et al. 2009).

398

399 When assessing the changes in the projected probability of occurrence of species in 2051–2080 vs.
 400 1971–2000 we used the arithmetic mean values of the three modelling methods. We calculated the
 401 absolute percentage change between the two time periods and proportional change in which the
 402 absolute percentage change has been divided by the probability of occurrence in 1971–2000. Then
 403 we calculated the arithmetic mean of percentage changes of species both in protected and
 404 unprotected squares. Next, we compared the statistical significance of proportional change in the
 405 probability of occurrence by using two-factor analysis of variance (ANOVA with Tukey's a
 406 posteriori test for pairwise comparisons), where the factors were the three boreal zones and
 407 protection status of squares (protected vs. unprotected). Proportional decrease and increase are not
 408 statistically strictly comparable as, for example, a doubling increase from a probability of
 409 occurrence of 50% gives a value of 100%, but a similar decrease to half of that yields 25%. To
 410 avoid this discrepancy in statistical tests, we used a logarithmic ratio (log ratio) of percentage
 411 changes, where, for example, 100% increase would be $\log(100/50) = +0.301$ and 50% decrease
 412 would be $\log(25/50) = -0.301$.

413

414

415 **Results**

416

417 The predictive accuracies of all generated BEMs (three modelling techniques times 100 species)
 418 were generally good or excellent, as only two species showed AUC values lower than 0.80
 419 (Appendix 4). In the Eurasian eagle owl *Bubo bubo* in GAM the AUC was 0.730 (fair) and in GLM
 420 0.686 (poor) and in the nightjar *Caprimulgus europaeus* in GAM the AUC was 0.786 (fair) and in

GLM 0.784 (fair). Kappa and TSS statistics showed largely similar patterns. The lowest kappa values were for the eagle owl (in GAM 0.330 and in GLM 0.297) and the aquatic warbler *Acrocephalus paludicola* (in GAM 0.316, in GBM 0.303 and in GLM 0.303) and in TSS for the eagle owl (in GAM 0.330 and in GLM 0.297) and the bearded parrotbill (in GAM 0.458 and in GLM 0.456) (see Appendix 4). When considering mean probability of occurrence, mire species were clearly northerly and marshland species southerly distributed (Appendix 5).

The probability of occurrence of all species combined decreased according to all scenarios, this decline being the greatest in southern boreal and the smallest in northern boreal zones with highly significant differences between the three zones (Tables 1 and 2). The probability of occurrence of species declined most according to the A2 scenario and least based on the B1 scenario, whereas BEMs based on the 19-model ensemble average for the SRES A1B suggested intermediate changes in climatic suitability.

The change in climatic suitability from 1971–2000 to 2051–2080 was highly significant between zones in forest, mire and marshland species (Table 2). Among marshland species, the probability of the occurrence of species increased, whereas among other species groups it generally decreased (Table 1). However, species-by-species inspection of the projected changes in the protected areas showed that among forest species, individual species trends can be rather contrasting (Fig. 3). For example, based on the 19-model ensemble scenario, the probability of the occurrence of forest species were projected to increase in protected squares in 16, 25 and 40 species and decrease in 35, 26 and 11 species in the southern, middle and northern boreal zones, respectively. In contrast, the suitability of climate in the protected squares was projected to decline for all species in mountain habitats and almost all species of mires, whereas almost all marshland species were predicted to benefit from the changing climate (Table 1, Fig. 3 and 4). Southern species such as the middle

spotted woodpecker *Dendrocopos medius* (not a breeding species in Finland, as yet) might expand their northern range boundary northwards whereas northern species such as the pine grosbeak *Pinicola enucleator* are likely to show shrinking ranges in the future (Fig. 5).

The probability of the occurrence of forest species declined noticeably in the southern boreal zone and increased in protected squares in the northern boreal zone, whereas that of mire species decreased clearly in all zones (Table 1, Fig. 3 and 4). The probability of the occurrence of forest species decreased significantly less or increased significantly more in protected than in unprotected squares according to the ensemble scenario and A2 scenario, and the pattern was also the same for the B1 scenario ($p=0.050$, Table 2). For mire species, according to A2 scenario the decline was more pronounced in unprotected squares. The probability of the occurrence of marshland species more than doubled in the middle boreal and northern boreal zones according to the A2 scenario. In the Arctic mountain species the probability of the occurrence of species declined based on A2 scenario by about two-thirds (proportionally over 80%, Table 1). The decline was more pronounced in unprotected squares.

The interaction between the two factors (zones and protection status in squares) was significant in the 19-model ensemble and the A2 scenario in all species combined, in forest species and in mire species (Table 2). The significant interaction implies that the values of the factors are not parallel. For example, in the ensemble scenario of forest species, the probability of occurrence increase more in protected than in unprotected squares in the northern boreal zone and decline less in protected squares than in unprotected squares in the middle boreal zone, whereas in the southern boreal zone the climatic suitability is projected to decline equally in protected and unprotected squares (Table 2).

Discussion

Potential broad-scale changes of species distributions in a network of protected areas have commonly been assessed by using data recorded on a grid system and fixed thresholds of the proportion of a protected area in a grid cell to determine areas where a given species is assumed to be protected (Araújo 2004; Kujala et al. 2011), or by using an index which calculates climate suitability and the proportion of a protected area in each cell (Alagador et al. 2011). We used a different approach here, as we connected the amount of specific habitat in each square and specifically in the conservation areas in it to species dependent on that particular habitat. The key reasoning for this is that the total conservation area in a given grid cell may provide misleading indications of the level of protection for a species, simply because a specific species group does not breed in a conservation area if its habitat is not available. A large proportion of protected habitat in the different zones was situated in our 5% hotspots of protected areas, varying between 29 and 79% between habitats and zones. Thus, we consider our approach of using 5% hotspots of protected habitats as a good representative of the overall protection of different habitats.

We used species of conservation concern as an indicator of the future value of protected areas. For the purposes of this study, we consider this choice more reasonable than including all the breeding bird species of Finland and adjacent areas into the analysis. This is because species which are under different environmental treats at present will very likely also be more vulnerable under future climate change. For example, persistence of species of agricultural areas and human settlements are not critically dependent on the conservation of natural habitats but more on other means such as measures supporting farmland biodiversity and developing biodiversity-friendly practices in urban planning. Moreover, a large proportion of forest species are habitat generalists occurring in various habitat types. The purpose of protected areas is to maintain biodiversity and for doing this, species

496 of conservation concern, which have declined largely due to human land use, are of primary
 497 importance (see Virkkala and Rajasärkkä 2007). However, we acknowledge that the situation in
 498 other biomes and geographic regions might be quite different due to lack of detailed knowledge of
 499 species and their habitat preferences. In the tropics most bird species vulnerable to climate change
 500 are not currently considered threatened (Şekercioğlu et al. 2012), and therefore the use of all
 501 species in analysing the future value of protected areas is reasonable. Altogether, we employed
 502 seven different classifications in order to delimit a group of species of conservation concern as
 503 diverse as possible. Using only one or two classifications might bias the species groups towards
 504 certain species and species traits.

505

506 In general, the climatically more suitable areas for the species were predicted to shift northwards,
 507 but the potential gain of southern species of conservation concern appears not to compensate for the
 508 loss of northern species. This was particularly clear in southern boreal Finland, where the projected
 509 overall decline in the probability of occurrence was the greatest. Many boreal species occurring
 510 particularly in the southern boreal zone are likely to lose climatically suitable areas and may thus be
 511 forced to shift their ranges towards the northern boreal zone. In our projections, this trend
 512 compensates for the overall loss in the northern boreal zone but it should be noted that the
 513 probability of occurrence of northern boreal species may drastically decline, which can be seen
 514 clearly in the Arctic mountain species, for example (see also Virkkala et al. 2008, 2010).

515

516 In contrast to our results, the bioclimatic envelope modelling studies conducted by Huntley et al.
 517 (2007) and Barbet-Massin et al. (2012) have suggested that bird species numbers in northern
 518 Europe including Finland will increase during the 21 century. The difference between those studies
 519 and the present one is that Huntley et al. and Barbet-Massin et al. have used all bird species in the
 520 modelling, while we included only species of conservation concern. Thus, the different delimitation

521 of the set of modelled bird species may in part explain the slight differences in the projected trends.
522 Moreover, in the study by Barbet-Massin et al. species richness was actually predicted to decline in
523 southern Finland, and increase only in northern Finland based on both climate and climate-habitat
524 variables combined. Thus, these results are in line with our study findings of a larger decline in the
525 probability of occurrence of species in the southern boreal zone in Finland than in the northern
526 boreal zone.

527

528 A BEM study carried out on the European scale suggested that protected areas may retain climatic
529 suitability of plant, mammal, bird and reptile species by 2080 better than unprotected areas (Araújo
530 et al. 2011). However, Araújo et al. (2011) noticed that Natura 2000 areas may not retain climatic
531 suitability any better or sometimes even less effectively than unprotected areas. They explained this
532 difference by the fact that national protected areas tend to be found more in mountains, which may
533 act as climate refugia. Natura 2000 areas are situated more often in flatlands where the proportional
534 range losses are projected to be greater (Peterson 2003; Loarie et al. 2009). In our study of bird
535 species of conservation concern, there was a tendency towards climatic suitability of declining less
536 in protected areas than in unprotected ones. Only in marshland bird species was the increase in the
537 probability of occurrence significantly greater in unprotected areas according to the B1 climate
538 scenario. Nevertheless, there was also an increase in marshland bird species in protected areas based
539 on this scenario. Thus, according to our analysis of bird species of conservation concern, protected
540 areas in Finland are not situated in suboptimal sites in relation to predicted climate change.

541

542 In the study of European protected area networks, Araújo et al. (2011) concluded that overall there
543 may be more winners than losers in Finland and Sweden in both vertebrate and plant species both in
544 national protected areas and in the Natura 2000 network in contrast with other European countries,
545 where losers predominate over winners. However, in our more detailed analysis of species of

546 conservation concern, the situation appears to be somewhat more pessimistic, and there are large
547 differences between habitats, such as between mires and marshlands. Araújo et al. (2011), however,
548 noticed that almost all of the subarctic and alpine species (97%) would lose climate suitability,
549 which is in line with the predicted decrease in the ranges of northern boreal bird species by 74–84%
550 by 2080 (Virkkala et al. 2008).

551

552 Human-caused direct land cover changes may noticeably affect the severity of the projected
553 changes of climate suitability for the species, as these factors often operate in a jointly boosted
554 manner (Travis 2003). The proportion of old-growth forests and virgin mires remains low due to
555 intensive forestry. Thus, old-growth forests and open mires remain isolated and fragmented,
556 situated mostly in protected areas, which further increases extinction probabilities of local
557 populations of species preferring these habitats.

558

559 The proportion of protected forests is clearly less in the southern and middle boreal zones than in
560 the northern boreal zone, which probably causes further difficulties for species preferring forest
561 habitats, such as old-growth forests, which will not persist in the managed forest landscape outside
562 protected areas. In mires, the south-north difference in the proportion protected is not as clear as in
563 forests, and in marshlands this proportion is even higher in the southern and middle boreal zones
564 than in the northern boreal zone. However, in the southern and middle boreal zones 70–80% of
565 mires have already been drained (Virkkala et al. 2000) and the direct habitat loss has been
566 considerable. Although northern boreal species are expected to disappear or decline drastically due
567 to climate change, the conservation biological value of a protected area network in the southern and
568 middle boreal zone will decline more than that in the northern boreal zone.

569

570 In addition, we have also included night-active species, such as many owls (e.g. the Eurasian eagle
571 owl, the Ural owl *Strix uralensis*) and the nightjar, for which the night (dark time) length is
572 probably a restrictive factor. Therefore, these species probably cannot extend their ranges towards
573 the northern, lighter latitudes during their breeding period to such an extent projected by the
574 bioclimatic envelope models. With all these other factors (land use, low proportion of protected
575 areas in southern and middle boreal zone, physical constraints) taken into account, our results of a
576 decreasing probability rate of occurrence of species are probably optimistic rather than pessimistic.

577

578 Habitats, of course, will ultimately change due to climate warming, but topography and
579 watercourses will largely define the occurrence and location of wetlands, for example, in the future.
580 However, the expected velocity of the habitat change is slower than the projected changes in the
581 climatically suitable areas for individual species. Boreal forests are expected to change by 2100 so
582 that southern Finland (the southern and middle boreal zones) is mostly covered by hemiboreal
583 mixed forests and only northern Finland (northern boreal zone) by boreal coniferous forests based
584 on generalized dynamic vegetation modelling (LPJ-GUESS) with two atmosphere-ocean circulation
585 models (AOGCMs; HadCM3 and NCAR-PCM, driven by SRES A2 emission scenario) (Hickler et
586 al. 2012). Arctic mountain heath vegetation was predicted to remain by 2100 only in north-west
587 Finland in the Scandian Mountains (see also Moen et al. 2004).

588

589 **Conclusions**

590

591 We have shown here that southern boreal protected areas may face, on average, surprisingly more
592 declines of species of conservation concern than northern boreal protected areas. Moreover, species
593 of southern boreal protected areas suffer from isolation and scarcity of a reserve network. Northern
594 boreal areas, on the other hand, are irreplaceable for preserving northern species from extinction,

because the northern species cannot move northwards owing to the Arctic Ocean acting as a dispersal barrier. The geographic location of a protected area network within a continent therefore also considerably affects the future efficiency of protected areas in maintaining biodiversity. An important issue is also that when analysing the significance of a protected area network in a grid scale, species-specific habitat preferences and habitat availability should be taken into account properly in order to study the efficiency of a protected area network in a changing climate.

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Table 1. Change in the mean probability of occurrence of the different species groups from 1971–2000 to 2051–2080 based on three different climate scenarios: B1 (CSIRO-MK3.0 GCM SRES B1 scenario), a 19-model ensemble average for the SRES A1B (19GCM) and A2 (MIROC3.2/medres GCM A2 scenario). The changes in probabilities of occurrence in the species groups are presented in the different vegetation zones in protected 5% hotspot squares and in unprotected, random squares. Absolute % change refers to change between the two time periods. In calculating proportional change, the absolute percentage change has been divided by probability of occurrence in 1971–2000.

Species group Scenario	Southern boreal % change		Middle boreal % change		Northern boreal % change	
	Proportional	Absolute	Proportional	Absolute	Proportional	Absolute
<u>All species</u>						
CSIRO, B1						
Protected	–12.9	–6.4	–7.1	–3.8	–2.5	–1.4
Unprotected	–12.5	–6.4	–8.0	–4.2	–4.0	–2.3
19GCM						
Protected	–17.8	–8.9	–9.7	–5.2	–7.7	–4.2
Unprotected	–17.5	–9.0	–11.8	–6.3	–12.9	–7.3
MIROC3, A2						
Protected	–32.1	–16.2	–19.5	–10.5	–14.7	–8.1
Unprotected	–32.1	–16.5	–22.7	–12.1	–20.9	–11.8
<u>Forest species</u>						
CSIRO, B1						
Protected	–13.7	–7.6	–5.6	–3.3	1.7	8.0
Unprotected	–13.9	–7.7	–7.5	–4.3	–0.4	–0.2
19GCM						
Protected	–21.1	–12.0	–6.8	–4.0	19.8	9.3
Unprotected	–20.9	–11.8	–10.7	–6.2	5.9	2.9
MIROC3, A2						
Protected	–38.6	–22.0	–20.4	–12.0	18.1	8.5
Unprotected	–37.8	–21.5	–26.3	–15.3	–0.5	–0.6
<u>Mire species</u>						
CSIRO, B1						
Protected	–27.6	–12.6	–20.7	–13.2	–8.0	–6.9
Unprotected	–25.9	–12.7	–20.4	–13.1	–9.5	–7.6
19GCM						
Protected	–45.5	–21.0	–43.5	–28.0	–29.8	–25.8
Unprotected	–45.0	–22.4	–43.4	–28.0	–32.5	–26.4
MIROC3, A2						
Protected	–62.2	–29.0	–62.8	–40.5	–52.0	–45.2
Unprotected	–63.4	–31.7	–62.9	–40.6	–54.6	–44.6
<u>Marshland species</u>						
CSIRO, B1						
Protected	12.8	4.2	22.7	5.6	14.2	2.5
Unprotected	15.3	5.3	25.1	6.3	15.7	2.8

19GCM						
Protected	43.1	14.4	73.9	18.0	66.9	11.9
Unprotected	44.4	15.4	75.9	18.8	73.2	13.2
MIROC3, A2						
Protected	50.3	16.4	122.3	29.3	155.7	27.8
Unprotected	48.4	16.5	125.7	30.7	159.7	28.7
<u>Mountain species</u>						
CSIRO, B1						
Protected	—	—	—	—	−7.9	−6.8
Unprotected	—	—	—	—	−12.6	−9.3
19GCM						
Protected	—	—	—	—	−59.5	−50.8
Unprotected	—	—	—	—	−66.6	−49.7
MIROC3, A2						
Protected	—	—	—	—	−81.0	−69.5
Unprotected	—	—	—	—	−85.0	−63.7

Table 2. Results of two-factor ANOVA (protection: protected vs. unprotected squares, and three vegetation zones) of proportional change according to each climate scenario in the different species groups. Original percentage change values were transformed as log ratio (see methods) for the tests. Pair wise significance is presented for the vegetation zones, 1 = southern boreal, 2 = middle boreal and 3 = northern boreal zone. Pair wise comparison based on Tukey's a posteriori test. Significance of interaction between the factors is presented.

Species group	Protection		Zones		Pair wise comparison	Interaction	
	F	P	F	P		F	P
All species							
CSIRO, B1	2.11	0.147	172.98	<0.001	3>2>1	1.86	0.157
19GCM	29.53	<0.001	149.41	<0.001	3>1, 2>1	13.45	<0.001
MIROC3, A2	39.52	<0.001	388.73	<0.001	3>2>1	12.81	<0.001
Forest species							
CSIRO, B1	3.85	0.050	162.32	<0.001	3>2>1	0.74	0.480
19GCM	87.89	<0.001	1513.25	<0.001	3>2>1	43.04	<0.001
MIROC3, A2	62.81	<0.001	907.68	<0.001	3>2>1	29.32	<0.001
Mire species							
CSIRO, B1	0.45	0.452	510.01	<0.001	3>2>1	4.18	0.016
19GCM	2.83	0.093	665.40	<0.001	3>2>1	7.11	0.001
MIROC3, A2	18.93	<0.001	443.54	<0.001	3>1, 3>2	3.79	0.022
Marshland species							
CSIRO, B1	9.94	0.002	74.57	<0.001	2>3, 2>1	0.30	0.743
19GCM	3.18	0.075	127.81	<0.001	3>1, 2>1	0.48	0.619
MIROC3, A2	0.386	0.535	435.61	<0.001	3>2>1	0.29	0.747
Mountain species							
CSIRO, B1	68.84	<0.001					
19GCM	7.04	0.009					
MIROC3, A2	4.78	0.031					

1 Legends to the figures

2

3 **Fig. 1.** A. Distribution of forests, mires, marshlands and Arctic mountain habitats in Finland based
4 on CORINE classification. B. Protected area network.

5

6 **Fig. 2.** Location of protected and unprotected squares in the different vegetation zones (dark green
7 = southern boreal, mid-green = middle boreal, light green = northern boreal): A. Forests, B. Mires,
8 C. Marshlands, D. Arctic mountain birch woods, E. Arctic mountain heaths.

9

10 **Fig. 3.** Probability (in %) of occurrence of species in protected squares in 1971–2000 and in 2051–
11 2080 based on the three climate scenarios. A. = southern boreal, B. = middle boreal, C. = northern
12 boreal zone. Species probability of occurrence is predicted to decrease below the diameter line and
13 to increase above the line.

14

15 **Fig. 4.** Change in mean probability (in %) between 1971–2000 and 2051–2080 according to the 19-
16 model ensemble (19GCM) scenario in the different zones in forest, mire and marshland species in
17 protected squares, A., B., C, and in unprotected squares, D., E. F., respectively.

18

19 **Fig. 5.** A. Distribution of the middle spotted woodpecker *Dendrocopos medius* in Europe according
20 to the European Bird Atlas (Hagemeijer and Blair 1997) in relation to the variation of the most
21 significant climate predictor variable for the species (maximum temperature of April–June in the 10
22 x 10' grid cells). B. Distribution of the pine grosbeak *Pinicola enucleator* in Europe in relation to
23 the most important climate predictor variable (growing degree days, maximum in the 10 x 10' grid
24 cells). C.-F. Predicted probability (in %) of occurrence of the middle spotted woodpecker in
25 protected and unprotected squares in Finland in 1971–2000 (C.) and in 2051–2080 (D.) and that of

26 the pine grosbeak in 1971–2000 (E.) and in 2051–2080 (F.). Prevalence (number of grid cells
27 occupied in the European atlas, 0.370 in the middle spotted woodpecker and 0.076 in the pine
28 grosbeak) was used as a cut-off value for the probability of presence in species occurrence.

Marshland species

Arctic mountain species

B

C

Forest species

2051-2080 (%)

A

B

C

Mire species

2051-2080 (%)

A

B

C

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