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RESEARCH
REVIEW

# Downscaling European species atlas distributions to a finer resolution: implications for conservation planning

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## ABSTRACT

**Aim** One of the limitations to using species' distribution atlases in conservation planning is their coarse resolution relative to the needs of local planners. In this study, a simple approach to downscale original species atlas distributions to a finer resolution is outlined. If such a procedure yielded accurate downscaled predictions, then it could be an aid to using available distribution atlases in real-world local conservation decisions.

**Location** Europe.

**Methods** An iterative procedure based on generalized additive modelling is used to downscale original European $50 \times 50$ km distributions of 2189 plant and terrestrial vertebrate species to *c.* $10 \times 10$ km grid resolution. Models are trained on 70% of the original data and evaluated on the remaining 30%, using the receiver operating characteristic (ROC) procedure. Fitted models are then interpolated to a finer resolution. A British dataset comprising distributions of 81 passerine-bird species in a $10 \times 10$ km grid is used as a test bed to assess the accuracy of the downscaled predictions. European-wide, downscaled predictions are further evaluated in terms of their ability to reproduce: (1) spatial patterns of coincidence in species richness scores among different groups; and (2) spatial patterns of coincidence in richness, rarity and complementarity hotspots.

**Results** There was a generally good agreement between downscaled and observed fine-resolution distributions for passerine species in Britain (median Jaccard similarity = 70%; lower quartile = 36%; upper quartile = 88%). In contrast, the correlation between downscaled and observed passerine species richness was relatively low (*rho* = 0.31) indicating a pattern of error propagation through the process of overlaying downscaled distributions for many species. It was also found that measures of model accuracy in fitting original data (ROC) were a poor predictor of models' ability to interpolate distributions at fine resolutions (*rho* = –0.10). Although European hotspots were not fully coincident between observed and modelled coarse-resolution data, or between modelled coarse resolution and modelled downscaled data, there was evidence that downscaled distributions were able to maintain original cross-taxon coincidence of species-richness scores, at least for terrestrial vertebrate groups. Downscaled distributions were also able to uncover important environmental gradients otherwise blurred by coarse-resolution data.

**Main conclusions** Despite uncertainties, downscaling procedures may prove useful to identify reserves that are more meaningfully related to local patterns of environmental variation. Potential errors arising from the presence of false positives may be reduced if downscaled-distribution records projected to occur outside the range of original coarse-resolution data are excluded. However, the usefulness of this procedure may be limited to data-rich regions. If downscaling procedures are applied to data-poor regions, then there is a need to undertake further research to understand the structure of error in models. In particular, it would be important to investigate which species are poorly modelled, where and why. Without such an assessment it is difficult to support unsupervised use of downscaled data in most real-world situations.

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**Keywords**

Complementarity, distribution atlas, downscaling, interpolation, generalized additive models, rarity hotspots, richness hotspots, ROC curve, reserve selection.

## INTRODUCTION

Distribution atlases provide a convenient representation of species distributions in near-equal-area grid cells on maps. Such representations have been widely used to study species-distribution patterns of abundance, rarity, richness, turnover and assemblage composition at varying spatial scales (e.g. Turner *et al.*, 1988; Williams *et al.*, 1999; Koleff & Gaston, 2002; van Rensburg *et al.*, 2002; Araújo, 2003). Atlas data have also been used to investigate and test the performance of different conservation-planning methodologies, such as reserve selection (e.g. Rebelo & Siegfried, 1992; Araújo & Williams, 2000; Williams *et al.*, 2000a; Araújo *et al.*, 2001; Araújo, 2004). However, there is a concern that the scale of most atlases is too coarse for real-world conservation planning applications (e.g. Stoms, 1992, 1994; Hopkinson *et al.*, 2000; Hulme, 2003; Rouget, 2003). In response to this problem there have been attempts to downscale species distributions to finer resolutions by combining remotely sensed data and expert opinion to assign species to habitats or land-cover classes thought to be suitable for species (Boitani *et al.*, 1999). One of the problems with this approach is that there may be insufficient expert knowledge of species–habitat relationships for many species and areas (e.g. Freitag *et al.*, 1998). In such cases the usefulness of expert-driven approaches may be limited to few well-known, often charismatic, species.

An alternative is to use empirical modelling techniques that explore the correlation between a response variable (e.g. species' occurrence records) and sets of environmental predictor variables (e.g. climate and land cover) to downscale distributions of species to another spatial resolution (e.g. Nix, 1986; Pearson *et al.*, 2002, 2004; Barbosa *et al.*, 2003; Stockwell & Peterson, 2003). Here we provide an example of such a procedure using one of the most powerful techniques available for modelling species distributions, generalized additive modelling (e.g. Bio *et al.*, 1998; Franklin, 1998; Pearce & Ferrier, 2000; Elith & Burgman, 2002; Thuiller *et al.*, 2003; Segurado & Araújo, 2004), to downscale original European plant, bird, mammal, reptile and amphibian species distribution atlas data from a $50 \times 50$-km grid to a finer 10′ grid resolution (i.e. *c.* $10 \times 10$-km grid). An attempt to evaluate European-downscaled distributions is undertaken by comparing downscaled predictions with observed fine-resolution distributions for passerine-bird species in Britain. The consequences of this downscaling at the European scale are further discussed by taking into account its effects on: (1) spatial patterns of coincidence in species richness; (2) distribution of richness, rarity and complementarity hotspots.

## DATA AND METHODS

### Species data

Coarse-resolution species data included 868,960 records of occurrence for different groups of European terrestrial vertebrates and higher plants. These comprised 187 mammal (Mitchell-Jones *et al.*, 1999), 445 breeding bird (Hagemeijer & Blair, 1997), 149 amphibian and reptile (Gasc *et al.*, 1997), and 2362 plant species (Jalas & Suominen, 1972–96). Data varied with regard to taxonomic coverage. Terrestrial vertebrates comprise all known species, whereas plants comprise *c.* 20% of the European flora (Humphries *et al.*, 1999). The grid used was based on the Atlas Florae Europaeae (Lahti & Lampinen, 1999), with cell boundaries typically following the 50-km lines of the Universal Transverse Mercator (UTM) grid, except near the border of the six-degree UTM zones and at coasts. Breeding bird, mammal, and herptile atlases used slightly different grid systems, including different rules to represent data on islands and coasts. Hence, they had to be converted to the AFE grid system by identifying unique (though sometimes approximate) correspondence between cells in these grids. The mapped area (2434 grid cells) included western, northern and southern Europe, but excluded most of the eastern European countries (except for the Baltic States) where recording effort was both less uniform and less intensive (for more details on data conversion see Williams *et al.*, 2000b).

Fine-resolution distributions included 132,826 records of occurrence for 81 passerine-bird species in Britain. These were used as a test bed for evaluation of downscaled models. The data were mapped on a $10 \times 10$-km grid and digitized from published atlases (Sharrock, 1976; Gibbons *et al.*, 1993). In order to reduce the effect of absences arising from natural interannual variability (Gates & Donald, 2000; Donald & Greenwood, 2001; Araújo *et al.*, 2002a) we considered grid cells as occupied if individuals were recorded in either one of the two recorded periods (i.e. 1968–72 and 1988–91).

### Climate and land-cover data

Climate and land-cover data included 20 variables interpolated for Europe in the context of the EC funded ATEAM project (http://www.pik-potsdam.de/ateam). All data were developed at a spatial resolution of 10′ for European grid cells based on the ATEAM geographical window and then aggregated to the Atlas Flora Europaeae $50 \times 50$-km grid. Climate data were averaged for the period of 1961–90 and included mean annual temperature, mean temperature of the coldest month per year, mean annual precipitation sum, mean winter precipitation sum, mean summer precipitation sum, mean annual growing degree days, mean ratio of annual actual over annual potential evapotranspiration. Selected climate variables include some of the most important determinants of physiological processes limiting distributions of species, especially amongst plants (e.g. Bartlein *et al.*, 1986; Woodward & Williams, 1987; Prentice *et al.*, 1992; Sykes, 1997).

The land-cover data were derived by aggregation of the PELCOM land-cover database. PELCOM is a 1-km pan-European land-cover database developed mainly from remotely sensed data. The classification methodology is based on a regional and integrated approach of the NOAA-AVHRR satellite data and ancillary information such as topographic features (Mücher, 2000). Although finer spatial resolution databases exist such as CORINE (CEC, 1993), PELCOM was selected because of its complete spatial coverage of the European window, and because of the homogeneity of the methodology used for the land-cover classification. PELCOM is also the most up-to-date of pan-European land-cover databases. The percentages of each land-cover class were calculated for each individual 10′ grid cell from the 1-km PELCOM cells. The data comprised four classes of land cover: forest, agriculture, urban and others. Forests were further subdivided into three classes: deciduous, coniferous and mixed forest. Agriculture was divided into two classes: the percentage of arable land and the percentage of grassland. The 'other' land cover class comprised: seminatural areas (divided into areas of shrubland, and barren land), inland waters, wetlands, permanent ice and snow and the sea.

### Downscaling process (all data)

Coarse-resolution European species data were randomly divided into a calibration (70%) and an evaluation (30%) data set. Species with less than 10 records in the calibration data were excluded from analysis so as to reduce errors associated with excessively small sample sizes (Stockwell & Peterson, 2002). Generalized Additive Models (GAM) (Hastie & Tibshirani, 1990) were then used to reproject the original 50 × 50-km grid distributions to a 10′ resolution (*c.* 10 × 10-km grid). The modelling process was implemented in an iterative fashion, as described in Table 1. In this process, stepwise GAM models were run on the calibration data set using climate variables, while residuals were regressed with land cover. Selected land-cover variables for every species were then added to the set of selected climatic variables to produce alternative models including land cover. This was necessary because stepwise models including all variables at once would only rarely select land-cover variables (see also Thuiller *et al.*, 2004a). The predictive accuracy of models using climate, or the combination of climate and land-cover variables, was assessed using the evaluation data set. Model accuracy was estimated with the area under the curve (AUC) index, based on the receiver operating characteristic (ROC) (Fielding & Bell, 1997). This index varies from 0.5 (random assignments) to 1 (accurate predictions) and represents the probability that the model correctly predicts the observed presences and absences. For each species, the model with greatest AUC was retained and used to downscale distributions to finer resolution. All analyses were performed with S-PLUS (Anon, 1999).

**Table 1** Iterative downscaling process; see text for more details

| Step | Rule or procedure |
|---|---|
| 1 | Run stepwise GAM using climate variables only |
| 2 | Run stepwise GAM on the residuals of step 1 using land cover as predictor variables |
| 3 | Run GAM using selected climatic and land cover variables in steps 1 and 2 |
| 4 | Compare predictive accuracies in models of steps 1 and 3 with ROC |
| 5 | For each species retain the model with better accuracy |
| 6 | Use retained models to reproject distributions at 10′ resolution |

### Assessing downscaled models (British passerine bird species)

The ability of models to downscale original European-species distributions to a finer resolution was examined by assessing the mismatch between downscaled and observed distributions of 81 passerine-bird species in Britain. A simple measure of similarity (Jaccard coefficient) was used: $S = C/A + B - C$, where $S$ is the similarity between two distributions, $C$ is the number of downscaled and observed species' distribution records that overlap, $A$ is the number of downscaled distribution records and $B$ is the number of observed distribution records. The similarity values range from 1 (complete overlap) to 0 (no overlap).

### Assessing consequences of downscaling for conservation planning (all data)

The consequences of downscaling were further investigated by examining models' ability to reproduce, at fine scale, the original observed patterns of richness, rarity and complementarity at the coarser scale. In particular, two kinds of comparisons were made: (1) Spearman rank correlations of species richness scores within and between groups; (2) analysis of the coincidence between hotspots for richness, rarity and complementarity before and after models are run.

Hotspots of richness were calculated as the $n$ top-ranking cells with highest sum values of species presence, while hotspots of rarity were calculated as the $n$ top-ranking cells with highest sum of species rarity values. Rarity values were measured as the sum of each species' inverse number of grid-cell records = $\Sigma(1/c_i)$, $i$: 0, $1 \leq i \leq n$, where $c_i$ is the number of grid cells occupied by species $I$ (e.g. Williams *et al.*, 1996; Araújo, 1999). Hotspots of complementarity (for usage of terms see also Dobson *et al.*, 1997; Araújo & Williams, 2001; Araújo *et al.*, 2002b), also known as maximum-coverage solutions (e.g. Church *et al.*, 1996), were calculated as combination of cells that maximized species representation for a given number of grid cells. To calculate these we used a heuristic technique adapted from the near-minimum-set algorithm of Margules *et al.* (1988). The algorithm starts by (1) selecting all areas with taxa that are equally or more restricted than the representation goal. For example, for a goal of representing each species at least once, it begins by selecting all areas that have species recorded in only one grid cell. Then (2) the algorithm follows a simple set of rules, applied iteratively to select areas richest in the rarest taxa. First it selects grid cells with the greatest complementary richness in just the rarest taxa (ignoring other taxa). If there are ties, (3) it proceeds by selecting areas among ties that are richest in the next-rarest taxa. If there are still ties, it then selects those areas among ties with the lowest grid-cell number (this is an arbitrary rule used in place of random choice among ties in order to ensure repeatability in tests). Finally these steps are repeated as necessary until the representation goal is achieved. A test is performed to reject any grid cell that in hindsight is redundant to the selected goal. A modified version of this algorithm was used to provide an approximation to a maximum coverage problem. For this purpose, we repeated steps one to three until the required number of areas was attained or exceeded. A final re-ordering of areas by complementary richness was made to provide an approximate solution to the maximum-coverage problem (Williams *et al.*, 2000b). To ensure comparability between hotspots selected with downscaled and non-downscaled distributions a similar area was selected for both cases. These included 100 hotspots for non-downscaled distributions and 2500 hotspots for downscaled ones (i.e. 100 hotspots × *c.* 50 km × *c.* 50 km = 2500 hotspots × *c.* 10 km × *c.* 10 km). Because there are usually a great number of equally efficient complementarity hotspot solutions we selected 10 solutions for each taxonomic group by breaking ties randomly (rather than by the lowest grid-cell number) within each run. Hotspots were identified with WORLDMAP software (Williams, 1999).

## RESULTS

### Model accuracy on interpolated coarse-resolution data (all data)

Generalized Additive Models trained on the 70% randomly selected calibration data set had a generally high accuracy, with AUC values above 0.9 (Swets, 1988) on the evaluation data set. Herptiles showed the highest AUC values (Mean = 0.95, SD = 0.05), immediately followed by plants and birds (Mean = 0.93, SD = 0.04 and 0.05, respectively) and then mammals (Mean = 0.91, SD = 0.05). The inclusion of land-cover variables increased the predictive accuracy of models in 26% of cases. Downscaled distributions recovered fine-resolution environmental gradients (e.g. altitudinal and land cover) that were not visible in the original coarse 50 × 50-km grid (Fig. 1).

### Model accuracy on downscaled data (British passerine-bird species)

There was a generally good agreement (median Jaccard similarity = 70%; lower quartile = 36%; upper quartile = 88%) between downscaled passerine-bird species distributions and observed fine-resolution distributions in Britain. The four examples provided in Fig. 2 illustrate different types of model performance. The downscaled distribution of Yellowhammer (*Emberiza citrinella*) was very coincident to its observed distribution ($S_j = 0.90$), with very few false positives (absent but predicted to be present) and false negatives (present but predicted to be absent) in the western and northern edges of its Scottish distribution. Likewise, the downscaled distribution of Raven (*Corvus corax*) displayed a good agreement with its observed distribution ($S_j = 0.70$). This level of agreement was coincident to the median level of agreement among the 81 passerine-bird species modelled. False positives and false negatives were recorded mainly in the eastern edges of its observed distribution. Downscaled and observed distributions for Black Redstart (*Phoenichurus ochruros*) and Wood Lark (*Lullula arborea*) showed levels of agreement below the lower quartile frequency distribution of similarity values ($S_j = 0.11$ and 0.04). However, a closer inspection of Fig. 2 reveals the existence of slightly different types of errors that are concealed by using a measure of similarity that does not distinguish the contribution of false positives and false negatives. For example, in the first case (Black Redstart *Phoenicurus ochruros*), downscaled distributions produced a great number of false positives but very few false negatives. In other words, the models predicted reasonably well the distribution of the environmental envelope occupied by the species in Britain but failed to account for additional factors shaping the distribution of absences in the real world. In the second case (Wood Lark *Lullula arborea*), downscaled distributions produced great numbers of both false positives and false negatives and very few modelled records overlapped with the observed records (i.e. few true positives). This is an extreme case of a model's inability to represent species' environmental envelopes in a particular region. Fortunately this level of failure was atypical and well below the lower quartile similarity values between modelled and observed distributions at the finer scale. However, by laying each species-distribution map on the top of each other we were able to compare patterns of downscaled and observed species richness. It was found that Spearman correlation coefficient (*rho*) between downscaled and observed species richness, at a fine resolution, was only 0.31. This is an indication that model error, although being low on average, propagates through the process of overlaying modelled distributions for many species.

We also assessed the degree to which accuracy of distribution models at coarse resolution (using AUC index with the ROC procedure) would predict accuracy of models at a fine resolution (using Jaccard similarity). We found there was no positive correlation (*rho* = −0.10) between Jaccard similarities (measuring how well models predict real distributions) and AUC values (measuring how well models fit the data). This observation provides an indication that assessments of model performance at one scale, such as those provided with the AUC index, may not yield suitable estimates of model performance at another scale.

### Conservation implications of downscaling (all data)

By excluding species with fewer than 10 records in the calibration data, we eliminated 28% (954 species) of species in the data: 36%

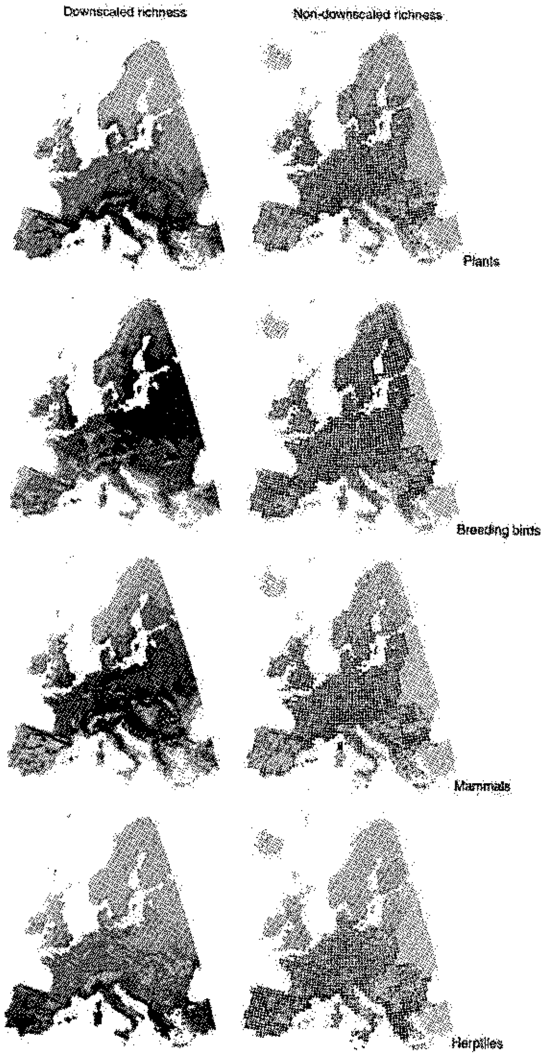

Figure 1 Species-richness scores among downscaled and non-downscaled distributions for plants; breeding birds; mammals; and herptiles. Species with fewer than 10 records in the calibration data sets for models are not plotted on the maps. We used a six class scale, where increasing intensities of grey represent increasing richness scores.

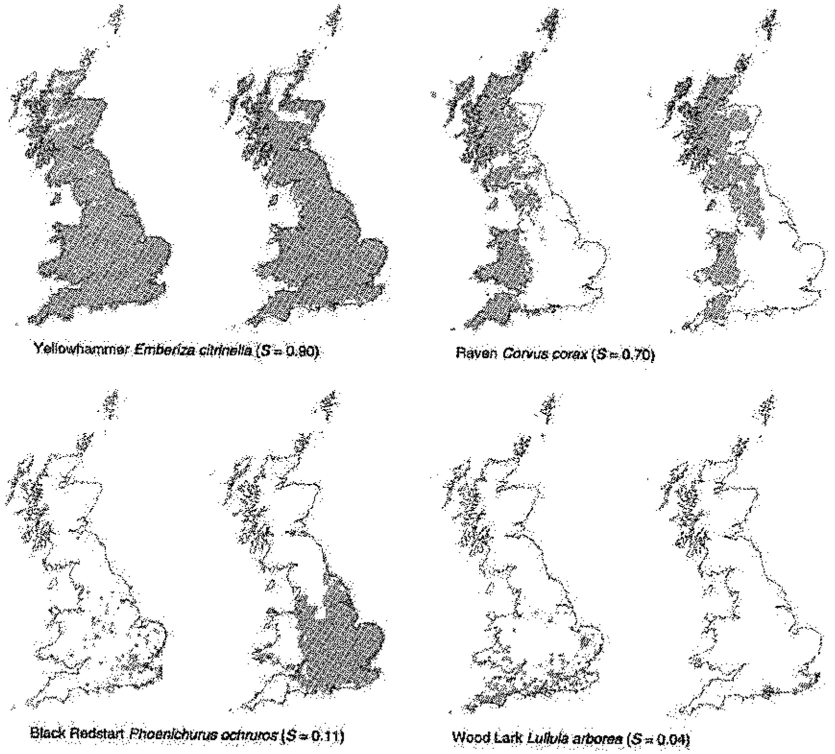
Yellowhammer *Emberiza citrinella* ($S = 0.90$)
Raven *Corvus corax* ($S = 0.70$)
Black Redstart *Phoenichurus ochruros* ($S = 0.11$)
Wood Lark *Lullula arborea* ($S = 0.04$)

Figure 2 Observed (maps on the left) and extrapolated (maps on the right) distributions for four passerine bird species in Great Britain: *Emberiza citrinella, Corvus corax, Phoenicurus ochruros*, and *Lullula arborea*. Values ($S$) indicate the degree of coincidence (Jaccard similarity coefficient) between observed and extrapolated distributions.

of plants (844 species), 12% of birds (55 species), 21% of mammals (40 species) and 10% of reptiles and amphibians (15 species). Exclusion of the rarest species in the original data did not affect overall patterns of richness within groups. That is, Spearman rank correlations between richness scores of data including all species and data excluding the rarest species was 1 for birds, mammals and herptiles and was 0.99 for plants. Species richness correlations between groups were also not greatly affected by exclusion of the rarest species, with cross-taxon correlations between plants (the group with the greatest proportion of excluded species) and the other groups being the weakest (Table 2a,b). Cross-taxon species richness correlations between downscaled group distributions shared the same broad patterns of coincidence in the original data, except for plants where a markedly different pattern emerged (Table 2b–c).

The consequences of excluding the rarest species from analysis were more important for reserve selection. Only richness hotspots were not greatly affected by this exclusion, with hotspots selected with all data coinciding between 88 and 100% with hotspots selected with exclusion of the rarest species (Table 3). A markedly lower level of coincidence was recorded for rarity hotspots and complementarity hotspots, where the degree of overlap ranged from 35 to 79% and 23–47%, respectively (Table 3).

Although the total area reserved was comparable between downscaled and non-downscaled hotspots the latter solutions were able to span a wider range of areas in Europe (Figs 3–5).

Table 2 Spearman rank correlation coefficients of species richness scores among groups of plants and terrestrial vertebrates in Europe with (a) original data including all species; (b) with modelled data excluding species with fewer than 10 records in the calibration set; (c) downscaled data excluding species with fewer than 10 records in the calibration set

| | Plants | Birds | Mammals | Herptiles |
|---|---|---|---|---|
| (a) | | | | |
| Plants | 1 | | | |
| Birds | 0.46 | 1 | | |
| Mammals | 0.75 | 0.63 | 1 | |
| Herptiles | 0.49 | 0.08 | 0.41 | 1 |
| (b) | | | | |
| Plants | 1 | | | |
| Birds | 0.49 | 1 | | |
| Mammals | 0.76 | 0.63 | 1 | |
| Herptiles | 0.42 | 0.09 | 0.41 | 1 |
| (c) | | | | |
| Plants | 1 | | | |
| Birds | 0.06 | 1 | | |
| Mammals | 0.64 | 0.61 | 1 | |
| Herptiles | 0.78 | −0.09 | 0.44 | 1 |

Table 3 Coincidence between hotspots selected with all species and with modelled species alone. For richness and rarity hotspots numbers are percentages of coincident hotspots. For complementarity hotspots numbers are mean percentages of coincident hotspots, after 10 simulations, while numbers within brackets are standard deviations to the mean

| | Richness hotspots | Rarity hotspots | Complementarity hotspots |
|---|---|---|---|
| Plants | 88 | 79 | 47 (1.7) |
| Breeding birds | 100 | 53 | 23 (2.3) |
| Mammals | 100 | 35 | 29 (4.3) |
| Herptiles | 96 | 49 | 29 (4.1) |

This is a logical consequence of using smaller but greater number of grid cells as units of selection, since poor-biodiversity areas within large grid cells are traded off by more targeted areas in smaller grid cells. Nevertheless, non-downscaled and downscaled distributions selected hotspots with a similar distribution in Europe. This was particularly evident for most of the hotspots selected with non-downscaled species data, which tended to be included by downscaled hotspots. In other words, if coarse-resolution hotspots were treated as a reference to validate fine-resolution hotspots, then results could be interpreted as showing that downscaled hotspots show a low false-negative (present but predicted to be absent) error rate. However, there were also some displacements in the location of downscaled hotspots in comparison to hotspots selected with coarse-resolution species data. This pattern, observed for hotspots selected with all three methods, indicates the existence of a variable false positive (absent but predicted to be present) error rate. Examples include selected complementarity hotspots for mammals that targeted sites in south-western Finland with non-downscaled distributions and in the eastern fringes of Norway with downscaled distribution data. Similarly, richness hotspots among non-downscaled bird distributions included areas in Bulgaria and Romania, while downscaled hotspots of richness excluded any area near these low latitudes. However, with our data it is difficult to interpret these displacements and understand whether they arise from errors in the models or they are a real consequence of planning reserves with finer resolution.

Another difference between non-downscaled and downscaled hotspots is their position relative to the major European gradients of altitude. For example, richness hotspots for mammals and plants had a tendency to concentrate on central European mountains like the Pyrenees, Alps, and Carpathians for both downscaled and non-downscaled solutions. However, non-downscaled solutions appeared to favour selection of richness hotspots on mountaintops (a probable artefact caused by the large grid-cell size), while downscaled solutions seemed to favour selection of mid-elevation sections of these mountains as predicted from empirical evidence that richness usually peaks at mid-elevations rather than mountain tops (Rahbek, 1995; Grytnes & Vetaas, 2002).

## DISCUSSION

We outlined a simple iterative procedure to downscale coarse-resolution distributions of large numbers of species to a finer resolution. The procedure is general as it does not imply a preference for any particular modelling technique. We used GAM but a variety of alternative techniques could have been used (e.g. Generalized Linear Models, Barbosa *et al.*, 2003; GARP, Stockwell & Peterson, 2003; Artificial Neural Networks, Pearson *et al.*, 2002, 2004). Indeed, two assumptions are common to all approaches used to downscale species' distributions to a finer resolution. The first is that governing processes affecting species' distributions at a coarse-resolution are also important to model distributions at a finer resolution. The second is that the correlation between a response variable (e.g. species distribution) and predictor variables (e.g. climate and land cover) provide a direct means to infer processes governing distributions of species. Naturally, these assumptions bear important caveats (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003) and departures from model assumptions are likely to vary for different species and regions. However, independently of the particular assumptions and parameterizations of each technique, it is important to recognize that any model involves some losses and gains of information. In the case of downscaling species distributions to a finer resolution the first loss refers to the almost unavoidable exclusion of restricted-range species from analyses (but see Kunin, 1998; He & Gaston, 2000; Kunin *et al.*, 2000). This is required because the empirical techniques used to interpolate distribution data are unable to handle species with only a few records with confidence (e.g. Stockwell & Peterson, 2002). In this study it was apparent that the exclusion of restricted-range species would have important implications for conservation planning. Indeed, the degree

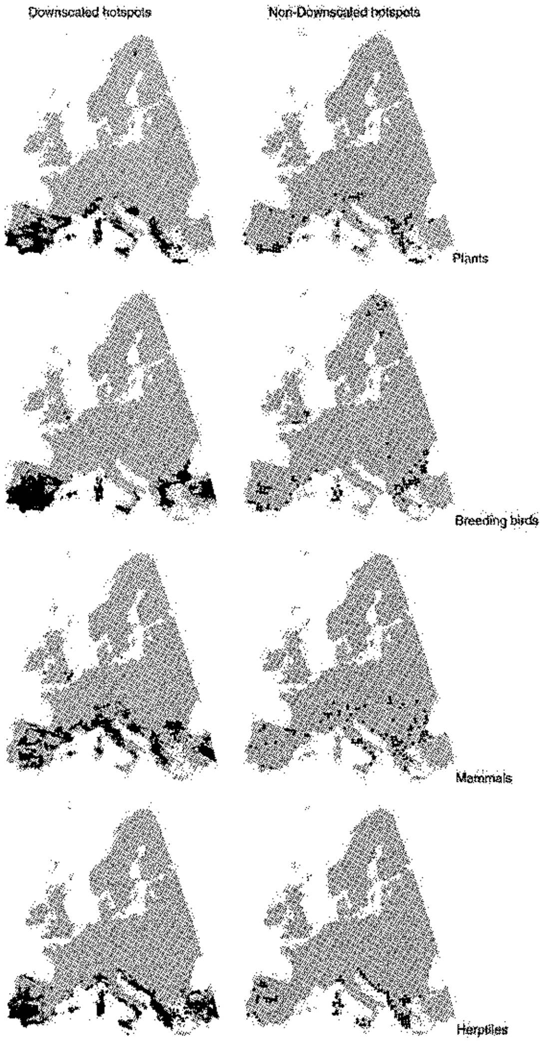

**Figure 3** Distribution of downscaled (10′ grid) and non-downscaled (50 × 50-km grid) rarity hotspots in Europe (see Methods).

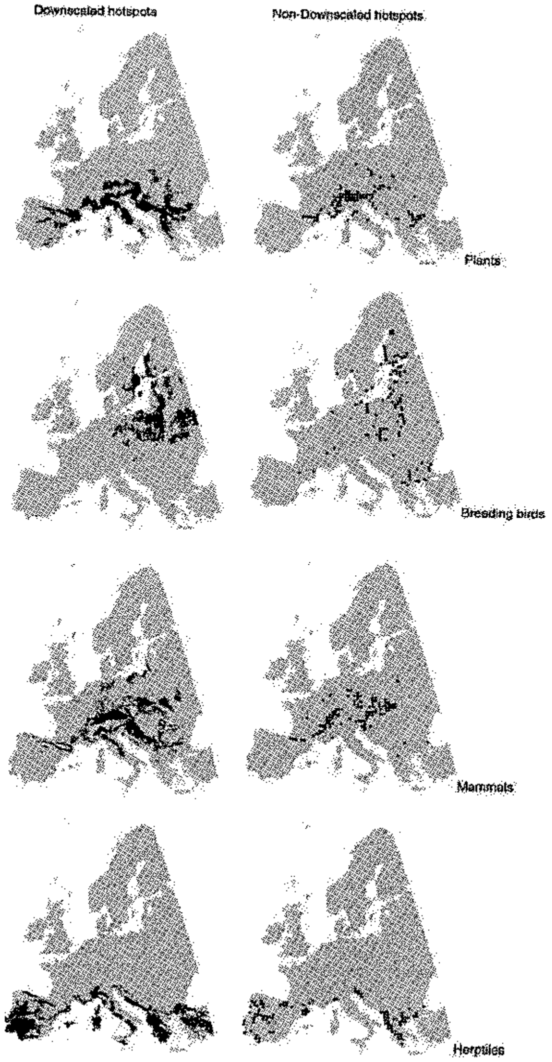

**Figure 4** Distribution of downscaled (10′ grid) and non-downscaled (50 × 50-km grid) richness hotspots in Europe (see Methods).

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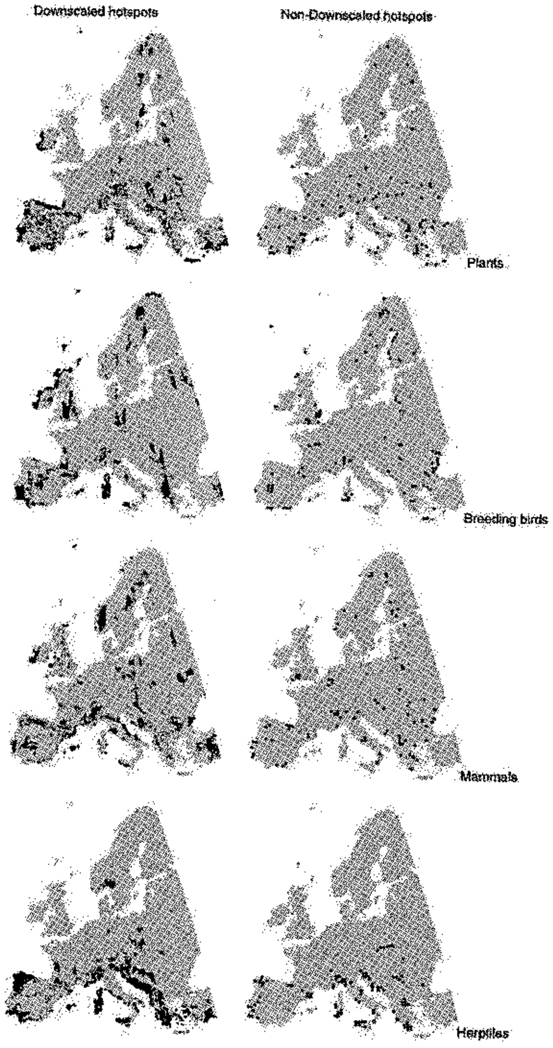

**Figure 5** Distribution of downscaled (10′ grid) and non-downscaled (50 × 50-km grid) hotspots of complementarity in Europe (see Methods).

of coincidence obtained when complementary hotspots were selected with all species or only the most abundant ones was very low, varying between 23% for breeding birds (SD = 2.3) and 47% for plants (SD = 1.7). A greater degree of coincidence between richness or rarity hotspots was recorded, although this is no great comfort as it is complementarity that is the most important pattern and it is this that requires prediction in conservation planning (e.g. Faith & Walker, 1996a,b; Williams *et al.*, 2000b; Araújo *et al.*, 2001, 2003, 2004).

The second loss of information is related to uncertainty of model predictions. It is generally accepted that original species' atlas distributions provide reliable estimates of presence (false positives are potentially low), although the same cannot be said about absences (false negatives are potentially high) (Araújo & Williams, 2000; Brotons *et al.*, 2004). Model predictions add a new degree of uncertainty given that the number of false positives increases to a variable but unknown extent, while the number of false negatives, although expected to diminish, remains unknown. This problem is particularly severe when models are utilized to interpolate observed distributions to a different resolution (the case of this paper), region (e.g. Peterson & Vieglais, 2001), or time (e.g. Thuiller *et al.*, 2004b), because model evaluation techniques are usually limited to the original circumstances upon which the models were built (e.g. Beutel *et al.*, 1999). Where models are used to interpolate distributions in a different resolution there is a possibility that the number of false negatives may increase for some species rather than decrease (e.g. the example of Wood Lark *Lullula arborea* in Fig. 2). Although in this study's particular assessment of passerine-bird species distributions such cases were a minority (i.e. below the lower quartile of the frequency distribution), it is still premature to generalize about the magnitude and frequency distribution of such errors. Even if there has been some progress in understanding the ecological and geographical factors underlying error in distribution models (Brotons *et al.*, 2004; Segurado & Araújo, 2004), there is little evidence that the behaviour of error remains constant across varying spatial resolutions. Hence, it would be particularly important to investigate the circumstances affecting model accuracy when interpolating distributions in a finer resolution. It is possible that systematic errors might be associated with particular kinds of geographical or environmental distributions of species (e.g. Segurado & Araújo, 2004), or that errors show a tendency to concentrate in particular sections of environmental space (Thuiller *et al.*, 2004b).

A major problem detected in this study was that assessments of model accuracy trained at the coarse resolution did not provide a good estimate of models' accuracy at the fine resolution, with AUC assessments of model accuracy for passerine distributions in Britain being not positively correlated with accuracy assessments based on direct comparison between observed and interpolated data (*rho* = −0.10). The problem may be more general and extend to situations where interpolations are made to different regions or times (for discussion see Oreskes *et al.*, 1994). An additional and often underestimated problem is that error of model predictions may accumulate through the process of overlaying modelled distributions for many species (Flather *et al.*, 1997). This pattern of error propagation was recorded in our particular evaluation of downscaled distributions of passerine-bird species in Britain. Here it was found that downscaled distributions had a generally good agreement with observed distributions (Jaccard similarity = 70%), but that the coincidence in species-richness scores between downscaled and observed distributions was only of 0.31 (*rho*). Although we could not perform such a detailed test for the remaining taxa and regions, we found, from visual inspection of the maps (see Fig. 1), that downscaled species-richness maps in Europe were generally able to recover original spatial patterns of richness at a coarse resolution. They were also able to identify fine gradients that were otherwise lost from the original coarse-resolution data. This is the case, for example, for the expected mid-elevation gradients of richness (e.g. Rahbek, 1995; Grytnes & Vetaas, 2002) that were clearly identified in the downscaled maps of richness and were lost in the original coarse-resolution maps of richness in Europe. Between-group downscaled patterns of terrestrial vertebrate species richness were also broadly coincident between downscaled models and original coarse-resolution data (except for plants), which further suggests that downscaling did not change the original structure in the data for these groups. Taken together these results provide grounds for optimism as to the usefulness of the overall downscaling procedure. If the approach is not able to predict accurately the distribution of all species at a finer scale, it can at least help in locating conservation areas that are more meaningfully related to environmental features of the land.

Despite the many uncertainties associated with modelling distributions at varying spatial scales (see also Thuiller *et al.*, 2003) the original problem remains wide open. There are now distribution atlases available for most parts of the world and their resolution is often too coarse for most conservation-planning applications. Furthermore, it is unlikely that the amount of resources available for undertaking extensive biological inventories will increase to the estimated *c.* $ 4.2 billion required to survey at least *c.* 20% of the land area (James *et al.*, 2001). Hence, the empirical downscaling of original coarse-resolution data is likely to remain one attractive procedure (e.g. Nix, 1986; Boitani *et al.*, 1999; Barbosa *et al.*, 2003; Stockwell & Peterson, 2003; Pearson *et al.*, 2004). Naturally, the usefulness of models to fill the gaps in our knowledge is open to debate (e.g. Slobodkin, 1988; Flather *et al.*, 1997). Given the losses and gains of information arising from downscaling procedures, the usefulness of the process is likely to be contingent on the goals and the ability to test results effectively. A critical issue for conservation planning is whether errors arising from accepting false positives (i.e. model predictions where species do not occur) are more severe than errors arising from ignorance of the local heterogeneity of species distributions within coarser-resolution grid cells. There are no established rules to find the appropriate trade-off between such opposing sources of error and the decision as to whether to use downscaled or original coarse-resolution data must depend on the goals of modelling and on a case by case assessment of risk. If false positives are a major problem, then a solution might be to exclude downscaled-distribution records that fall outside the geographical

range of the initial coarse-resolution data. This would minimize the risk of making wrong decisions with interpolated data. Naturally this solution is likely to be more useful in data-rich regions (e.g. Europe) where original coarse-resolution data cover the full extent of the distribution of species. In data-poor regions, where coarse resolution data may consist of unrealistic range-filling maps (which conceal species environmental relationships required to model distributions) or an incomplete coarse-resolution coverage of species distributions, excluding records that fall outside the range of the original coarse-resolution data may limit the usefulness of the downscaled predictions.

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