SPECIES: A Spatial Evaluation of Climate Impact on the Envelope of Species

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Abstract

A model, A Spatial Evaluation of Climate Impact on the Envelope of Species (SPECIES), is presented which has been developed to evaluate the impacts of climate change on the bioclimatic envelope of plant species in Great Britain. SPECIES couples an artificial neural network with a climate–hydrological process model. The hybrid model has been successfully trained to estimate current species distributions using climate and soils data at the European scale before application at a finer resolution national scale. Using this multi-scale approach ensures encapsulation of the full extent of future climate scenarios within Great Britain without extrapolating outside of the model’s training dataset. Application of the model to 32 plant species produced a mean Pearson correlation coefficient of 0.841 and a mean Kappa statistic of 0.772 between observed and simulated distributions. Simulations of four climate change scenarios revealed that changes to suitable climate space in Great Britain is highly species dependent and that distribution changes may be multidirectional and temporally non-linear. Analysis of the SPECIES results suggests that the neural network methodology can provide a feasible alternative to more classical spatial statistical techniques. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Species’ distributions; Climate change; Artificial neural networks; Spatial scale

1. Introduction

It is widely accepted that natural distributions of flora and fauna are determined primarily by their environmental requirements (Woodward, 1987; Huntley, 1999). This generalisation is true at a variety of spatial scales, with different environmental factors of greater importance at different scales. It is expected that climatic forcings are of increasing importance as scale increases, from the regional, through national, continental, to the global. This paper reports the development of a scale independent model (SPECIES), based around coupling an artificial neural network (ANN) with a climate–hydrological process model, which is able to identify bioclimatic envelopes and predict changes to the potential distribution of species under a range of climate change scenarios. The usefulness of the climate envelopes approach has been challenged by the identifica-
tion of the importance of dispersal and inter-species interactions in determining species ranges (Davis et al., 1998). However, this paper confirms the validity of the climate envelopes approach for identifying certain characteristics of the complex environment–biota relationship, especially at national and continental scales where the importance of climatic forcings are shown to be high.

There has been growing concern in recent years about the potential effects of climate change on species and ecosystems. Anthropogenic climate change is expected to result in globally-averaged increases in air temperature of 1.4–5.8 °C by 2100 relative to 1990 (IPCC, 2001). This warming would be accompanied by seasonal changes in precipitation, radiation, potential evapotranspiration and other climatic regimes (Hulme and Jenkins, 1998). Such changes in climate have the potential to greatly impact the distribution of species and therefore habitat composition, with species expected to respond individually to climate change (Huntley, 1999).

These concerns have led to the development of a number of predictive models (Prentice et al., 1992, 1993; Huntley et al., 1995; Haxeltine and Prentice, 1996; Sykes et al., 1996). The models can be classified as either static, providing time-independent equilibrium predictions as a function of environmental variables, or dynamic, predicting time-dependent responses to a changing environment (Prentice and Solomon, 1991). Models within these categories may then be either correlative, based on correlations between environmental variables and species’ distributions, or mechanistic, aiming for a physiological simulation of the mechanisms defining a species’ response to climate (Beerling et al., 1995).

The use of static correlative models based around the concept of climatic envelopes (Box, 1981) has become one active area of study. Notably, Huntley et al. (1995) used climate response surfaces to define bioclimatic envelopes based upon three environmental variables. A major advantage of such models is that there is no requirement for detailed physiological data of individual species. Instead, static correlative models utilise the considerable field data available for species presence/absence at the national and continental scales, making the model applicable to a wide variety of species.

The potential use of ANNs for characterising bioclimatic relationships has been discussed and tested by Hilbert and van den Muyzenberg (1999) and Hilbert and Ostendorf (2001), and is further explored in this paper. ANNs are computer systems, inspired by the structure and operation of the brain, that have the ability to ‘learn’ output data from sets of input patterns. Such systems have been widely employed in the physical and chemical sciences, but have only relatively recently been applied in the environmental field (e.g. Lek et al., 1996; Lek and Guegan, 1999; Manel et al., 1999; Zealnd et al., 1999; Chon et al., 2000; Karul et al., 2000; Brosse et al., 2001; Lusk et al., 2001). This study used a feed-forward ANN with backpropagation (see Section 2.3). For detailed descriptions of the mathematical principles of feed-forward and other types of ANNs see Tarassenko (1998) and Picton (2000).

The use of neural networks for simulating species’ distributions offers a number of advantages over more classical statistical modelling techniques. Firstly, the methodology enables the incorporation of input variables from multiple sources, such as categorical or boolean data. For example, Hilbert and Ostendorf (2001) included both categorical (soil parent material classes) and non-categorical (climate parameters) variables as inputs into an ANN. SPECIES currently uses five environmental inputs and can easily be adapted to accommodate more (or different) inputs, such as dominant land-cover classes. Secondly, the neural network does not assume a normal distribution of the data and is thus able to determine climatic envelopes that have non-linear responses to environmental variables. This makes the technique useful for identifying ‘patchy’ or sparse distributions, for example where an unusual combination of environmental factors may make a habitat suitable for the species under investigation. Thirdly, the ANN is robust to ‘noise’ in the training dataset (Dawson et al., 1998). This should account for those errors in the species’ distribution data whereby the ab-
ence of a species at a particular location is no guarantee that it does not exist there, only that it has not been sited by an observer.

A notable disadvantage of ANNs is the large quantity of data required to train, validate and test the network. This limitation has been minimised by using extensive datasets available for European climate, soils and species distributions (the European dataset consists of 4688 grid samples). A further disadvantage is that causal relationships between species distribution and environmental data are not immediately identified in ANNs, but require further procedures, such as weight analysis, to identify (Manel et al., 1999).

The SPECIES model was initially developed for studying plant species’ distributions and has currently been used to model 32 species selected from a variety of habitat types in Britain (montane, upland hay meadow, heathland, blanket and raised bog, salt marsh, coastal grazing marsh, fens and cereal field margins). This paper describes the details of the modelling methodology and summarises model performance. Results for two illustrative plant species are presented; *Rhynchospora alba* (white-beaked sedge) and *Salix herbacea* (dwarf willow).

2. Methodology

A schematic showing the main elements of the modelling process is presented in Fig. 1. A climate–hydrological model is used to pre-process input climate and soils data to derive relevant climatic variables of biological importance (bioclimatic variables) for input to the neural network. The model integrates these bioclimatic data to predict the distribution of species through the characterisation of bioclimatic envelopes (areas which are potentially suitable for a species in terms of climate). An important element of the methodology is that ANN training is carried out at the European scale so as to include the full climate range of a given species. The model is then downscaled to a finer resolution in its application to Great Britain. This ensures that, when applied to future climate scenarios, the network is not used to extrapolate outside its training dataset.

2.1. Climate and soils databases

A 1961–1990 mean monthly climatology for the European region extending from longitude
11°W to 42°E and from latitude 35 to 66.5°N was available at a resolution of 0.5° latitude/longitude for a suite of seven surface climate variables: minimum, maximum and mean air temperature; precipitation totals; sunshine hours; vapour pressure; and wind speed (Hulme et al., 1995). This climatology was constructed from observed station data distributed across the region. The interpolation of the station data to the grid used mean elevation for each 0.5° grid as one of the predictor variables. Potential evapotranspiration was estimated from this dataset using the Penman formula (Penman, 1948) by Harrison and Butterfield (1996).

Observed mean monthly climatic data for the 1961–1990 normal were also available for Great Britain at a 10 km resolution for all the variables listed for Europe (Hulme and Jenkins, 1998). The resolution of this dataset has been increased to 5 km so as to match the higher resolution soils data by sub-dividing each 10 km grid cell into four.

Data on the available water-holding capacity of the soil (AWC) at a 0.5° latitude/longitude resolution for Europe were estimated using the database and methodology of Groenendijk (1989). This method calculated AWC from soil type, texture, slope, stoniness and lithic contact for the three predominant soils in each grid cell using simple pedo-transfer functions and look-up tables. AWC data for Great Britain were obtained from the UK Climate Impacts Programme for the dominant soil type in each 5 km grid cell.

2.2. The climate–hydrological model

Environmental inputs which are thought to have direct physiological roles in limiting the ability of plants to survive and grow have been calculated from the climate and soils data at both European and British scales within a climate–hydrological process model. Five variables, based on the fundamental requirements of temperature and moisture, were used as inputs to the ANN:

2.2.1. Absolute minimum temperature \(T_{\text{min}}\)

Low temperatures affect the survival of woody plants with different cold tolerance mechanisms (Haxeltine and Prentice, 1996) and the transition from vegetative to reproduction development in other plants (Gallagher, 1986). They can also result in frost kill for plants in areas with extremely cold winters. Woodward (1987, 1988), Raison et al. (1979), Prentice et al. (1992, 1993) and others have emphasised the significance of minimum temperatures in determining species’ distributions, with \(T_{\text{min}}\) generally acknowledged as being the preferred variable (Sykes et al., 1996; Haxeltine and Prentice, 1996; Woodward and Rochefort, 1991). \(T_{\text{min}}\) is the theoretical absolute minimum temperature over a 20 year period and is calculated from the mean temperature of the coldest month in any one year \(T_c\) in °C according to the equation:

\[
T_{\text{min}} = 0.006 T_c^2 + 1.316 T_c - 21.9
\]

(after Prentice et al., 1992)

2.2.2. Maximum annual temperature \(T_{\text{max}}\)

Plants can be damaged beyond an upper temperature threshold and high temperatures are known to have important effects on the rate of respiration versus photosynthesis (Woodward, 1987) and pollination (Wheeler et al., 1996). The maximum temperature of the warmest month was used as a surrogate for maximum temperature.

2.2.3. Growing degree days (GDD)

The seasonal cycle of temperature affects the potential length of the growing season and the rate of plant development (Harrison, 1999). The relationship between development rate and temperature is often quantified in terms of GDD, which is used as an index of the energy available for completion of the annual life cycle (Woodward, 1987; Prentice et al., 1992). Annual GDD (day °C) is calculated as:

\[
\text{GDD} = \sum \max\{0, (T_m - T_t)\}
\]

where \(T_m\) is the mean daily temperature (obtained from the monthly averages by sine curve interpolation between mid-months to obtain quasi-daily values; Brooks, 1943; Harrison et al., 2000) and \(T_t\) is the threshold minimum temperature for growth. It is common to use a \(T_t\) value of either 0 °C (Woodward and Rochefort, 1991) or 5 °C (Prentice et al., 1993; Beerling et al., 1995; Huntley et
A threshold value of 5 °C is considered to be of most significance for plants in Europe’s temperate climate and was adopted in this study.

2.2.4. Soil moisture surplus (SMS) and soil moisture deficit (SMD)

Soil water availability, as mediated by the balance between precipitation (ppt), potential evapotranspiration (pet) and a soil’s AWC, is known to have a strong influence on plant growth (Woodward, 1987; Prentice et al., 1992). Indeed, water shortage is probably the most important factor affecting variations in plant growth rates across Europe (Harrison, 1999). Two input variables, accumulated annual surplus and deficit, have been derived using a two-layer bucket-type water balance model. Firstly, the available water for each month (aw) is calculated as ppt–pet. The soil water reserve (rs) for each month is calculated to yield either a surplus or a deficit: if in the first month aw is positive then this becomes the rs, up to a maximum of the AWC, any excess above the AWC is assigned as the surplus. If aw is negative then rs is reduced by that amount (to a minimum of 0), and aw is equal to a deficit. The same rules are applied in successive months and an accumulated surplus and deficit is calculated for the year, yielding the model input variables SMS and SMD.

2.3. Supervised training of the neural network

The current European species’ distribution was obtained as presence/absence data and mapped to a 0.5° grid for use as the target output during network training. The primary source of distribution data has been the digitisation of maps from Meusel et al. (1965, 1978, 1992), though several distributions from the Atlas Flora Europaea (Jalas and Suominen, 1972–1991) were obtained in digital format (Lampinen, personal communication, 2000). The presence or absence data was converted into a smoothed distribution using a Kriging interpolation procedure (Oliver and Webster, 1990). This smoothing assisted network training by ensuring that at range margins ‘presences’ (a value of 1) do not neighbour ‘absences’ (value of 0) when climatic conditions in neighbouring grid cells are similar at this course spatial scale. Smoothing also reduced the influence of sampling error, whereby a species does occur in a grid cell but has not been identified there. The smoothed distribution was thus used to provide a representation of the species’ climate envelope in Europe and was used as the target output during network training.

Before proceeding with ANN training, the environmental inputs were normalised using a linear transformation based on the minimum and maximum values for Europe (Tarassenko, 1998). Normalisation was applied because the input variable ranges differed by orders of magnitude and transformation made the variables cover the same range. The full European dataset was then split into three randomly selected and equally sized parts for network training, validating and testing. The training set was back-propagated through a feed-forward network with 5 input nodes, 11 nodes in a single hidden layer, and one output node. Network architecture and parameter values were chosen as those providing best relative performance during preliminary investigations (Pearson, 1999). Models were constructed and trained using SNNS (Stuttgart Neural Network Simulator) version 4.1 software (University of Stuttgart, Germany). Network training employed a sigmoidal activation function and a quadratic (mean squared) error function to compare the output signal with the target output (Maier and Dandy, 1998). Connection weights were adjusted using a backpropagation learning algorithm (generalised delta-rule), with weights updated after every training pattern (SNNS user manual v4.1, University of Stuttgart). Initial connection weights were selected randomly in the range 2.0 to −2.0, and the learning parameter set at 0.2. No momentum term was used since network training time was not problematic.

The validation set was not used directly for updating weights during network training but was used to monitor network error (every 100 cycles), enabling identification of when the network began to overgeneralise. Network training was stopped when the error on the validation set reached a minimum. This avoided over-training the net-
work, whereby the network learns the details of the training data rather than the underlying relationship between inputs and outputs (Tarassenko, 1998). For each species multiple (at least three) training runs were performed, each with different random weight initialisations. This was necessary since there are many local minima in weight space and different random initialisations will therefore produce different weight sets when training is stopped. The optimal network for each species was selected as that achieving the lowest minimum validation set error.

3. Results

3.1. Model testing

The trained network was tested on the unseen third of the full European dataset. Forward propagation of the test set once through the network gave predicted values which were correlated against the target (actual) outputs. Calculation of the Pearson correlation coefficient for the 32 modelled plant species showed a high relationship between predicted and target outputs (mean $r = 0.841$, maximum $r = 0.948$, minimum $r = 0.605$).

A more comprehensive test of the model was provided by evaluating its accuracy in simulating the observed species’ distribution. The full European dataset was thus propagated through the trained network and the outputs mapped. Due to the distribution smoothing, it was necessary to determine a cut-off threshold value for occurrence (above which values were taken to represent ‘presence’) that best represented the actual distribution. This was achieved through calculation of Cohen’s kappa statistic of similarity ($k$) (Light, 1971; Monserud and Leemans, 1992) at thresholds increasing in increments of 0.1 until maximum agreement between observed and simulated distributions was identified. Kappa provides a measure of proportional accuracy, adjusted for chance agreement, and has been recommended as an effective and appropriate statistic for evaluating and comparing presence–absence models (Manel et al., 2001). There are some concerns that kappa may be affected by low prevalence (Ridourn and Heath, 1999) and may overestimate the degree of chance agreement (Foody, 1992). However, Manel et al. (2001) found little evidence of the effect of low prevalence and suggest that kappa remains a superior test to the more widely used calculation of percentage success at predicting presences, which does not take into account chance agreement or prevalence effects (Fielding and Bell, 1997). Maximised values of $k$ were found to range from 0.957 down to 0.360 (mean $k = 0.772$). The threshold value for occurrence ranged in value from 0.2 to 0.8, with a mode of 0.5.

According to Monserud and Leemans’ (1992) subjective guidelines, kappa values above 0.7 can be considered to indicate ‘very good’ agreement. Simulated distributions were thus found to exhibit high levels of agreement with the observed distributions in the majority of cases. Figs. 2 and 3 show observed and simulated European distributions for the example species Rhyynchospora alba (white-beaked sedge) and Salix herbacea (dwarf willow). R. alba is distributed throughout much of northern Europe with a southern limit extending from northern Spain to northern Ukraine, and with notable absences from western Britain and inland Scandinavia. S. herbacea is found in montane arctic-alpine habitats, notably the highlands of Scotland, the Alps, the Pyrenees and Scandinavia. For each species, major distribution limits and population clusters were identified.

Having trained and tested the ANN at the European scale, the model was then downscaled to Great Britain. Propagating the British environmental inputs (11 180 grid cell samples) through the network, and applying the threshold values already determined, allowed the current suitable climate space for a species to be simulated at the higher resolution.

The simulated British distributions were found to identify principal trends in the observed distributions for the 32 species modelled, though accuracy of the simulations was reduced compared to those for the whole of Europe. Example results for R. alba and S. herbacea (Figs. 4 and 5) demonstrate the general tendency to simulate more fragmented climate spaces at the finer resolution. The simulated distribution of R. alba re-
produced the observed trend towards presences in the west of Britain and the south east, but did not identify actual presences in parts of western England. For *S. herbacea*, the simulated distribution accurately identified presences in Scotland and the Lake District, but overpredicted the distribution in Wales and showed suitable climate space in the higher parts of south west England where no actual presences were recorded. Such differences between coarse-resolution observed distributions and downscaled simulated distributions are to be expected since more localised climatic variation is captured in the higher resolution dataset whilst factors other than climate, such as land-use and habitat availability, will be of increasing importance as scale is reduced.

3.2. Predictions under future climate change

The trained model was used to predict changes in the climate envelopes of species in Great Britain based on a range of climate change scenarios. Four scenarios have been developed for Great Britain by the UK Climate Impacts Programme termed Low, Medium–Low, Medium–High and High (Hulme and Jenkins, 1998). All
four scenarios were based on the GCM experiments undertaken at the UK Hadley Centre for Climate Prediction and Research using the HadCM2 model (Mitchell et al., 1995; Johns et al., 1997; Mitchell and Johns, 1997). Each scenario has been constructed for three time periods (the 2020s, 2050s and 2080s) based on an average of 30 years of data. The Low and High scenarios for the 2020s and 2050s have been utilised in this study. These reflect the extremes in the uncertainty in future global warming rates attributable to different climate sensitivities and greenhouse gas emissions scenarios from the IPCC Second Assessment Report (IPCC, 1996). Changes in UK mean temperature are predicted to be in the order of 0.1 °C per decade for the Low scenarios up to 0.3 °C for the High scenarios.

The climate change scenarios were applied to the climate–hydrological model to compute future bioclimatic input variables. These were then

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Fig. 4. Simulated UK distribution of *R. alba* (5 km national grid), presented with the observed distribution (0.5° latitude/longitude).

Fig. 5. Simulated UK distribution of *S. herbacea* (5 km national grid), presented with the observed distribution (0.5° latitude/longitude).
propagated through the neural network to give potential future species’ distributions in Britain, again on a 5 km grid. Simulations for the 32 species modelled revealed responses that were highly species dependent, with the degree of change varying greatly. The expected trend of northward expansion of suitable climate space for many species was apparent, though northward migration of available climate space leads to contracting British distributions for those species that currently favour more northern climates. The distribution changes tend to be multidirectional and are often temporally non-linear, with a species potentially able to move into an area under the 2020s scenario before that climate space is lost under 2050s warming.

Results for *S. herbacea* under the four climate change scenarios demonstrate these trends (Fig. 6). The Low scenario for the 2020s shows suitable climate space being lost from Dartmoor, lowland Wales, north west and north east England. This pattern of change continues under the 2050s Low scenario. Under the High scenario for the 2020s only parts of Snowdonia, the Pennines, the Cheviots and the Lake District remain suitable in England and Wales. The 2050s High scenario indicates the loss of all potentially suitable climate space in Wales and a restricted distribution elsewhere. In Scotland, under the High scenario for the 2020s there is suitable climate space through-out almost all the Grampians, Highlands and islands, although most of this new area is lost under the 2050s High scenario.

### 4. Discussion and conclusion

The current model has performed well at identifying climate envelopes at the European scale, with a mean kappa value of 0.772 calculated between observed and simulated distributions for 32 species modelled. Results are comparable with those from similar bioclimatic modelling studies carried out at the European scale and to the same 0.5° resolution: Huntley et al. (1995) achieved a mean kappa agreement of 0.701 between observed and simulated distributions for eight higher plants, whilst Beerling et al. (1995) identified a kappa value of 0.691 using similar statistical methods for the species *Fallopia japonica*.

Downscaled model outputs have indicated those regions in Britain with potentially suitable climate space for each species. The reduced accuracy in simulating actual British distributions is to be expected from the postulation that the importance of climate in influencing species’ distributions decreases as scale decreases. Thus, a likely reason for reduced accuracy is the increasing influence of localised land-use and micro-climatic factors (including aspect) as scale reduces.
The modelling approach has also highlighted an archetypal data scaling problem. All gridded data is inevitably averaged out over a given area, such that when moving to a higher spatial resolution more local variation is apparent in the data. Consequently, magnitudes are greater at the smaller scale. Thus, in identifying suitable model inputs, it has been necessary to select variables that do not fall outside the European maximum and/or minimum when downscaled to Great Britain. This demonstrates that though the model itself may be regarded as scale independent, the data is not.

It is proposed that ANNs are a feasible alternative to more traditional biogeographical modelling techniques, though the methodology has a number of limitations. Firstly, the model does not take into account the possible physiological effects on plants of future increases in the atmospheric concentration of CO₂, commonly termed the CO₂ ‘fertilisation’ effect. This effect remains very difficult to quantify but it is not estimated that it will result in any significant shifts from the modelled potential distributions (Melillo et al., 1993; Houghton, 1997). Secondly, the validity of the model’s training dataset is based on the assumption that current species’ distributions are in equilibrium with the current climate. This assumption is supported by the success achieved in simulating current distributions from climate data.

A third important limitation is that whilst the model identifies areas that will become climatically suitable for a species under future climate change, no account is taken of factors that may limit species dispersal. Limiting factors include migration rates (Huntley, 1991; Melillo et al., 1996), barriers to migration (including urban areas and agricultural land-use) and inter-species competition as ecosystems change in composition (Bazzaz, 1996; Davis et al., 1998).

Such limitations demonstrate the complexity of the natural system and it is recognised that climate is only one of a number of factors that will influence the future ranges of species. Nevertheless, the model presented provides an indication of the magnitude of the impacts of future climate changes and offers an insight into potential future trends, including the identification of those regions and species that are most susceptible to change. A challenge for future research will be to develop an integrated approach, incorporating factors such as land-use change and dispersal mechanisms, so as to enable a fair simulation of species’ distribution changes within the boundaries of suitable future climate space.

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