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Modelling climate change impacts on species' distributions at the European scale: implications for conservation policy

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ABSTRACT

The availability of suitable climate space across Europe for the distributions of 47 species chosen to encompass a range of taxa (including plants, insects, birds and mammals) and to reflect dominant and threatened species from 10 habitats was modelled for the current climate and three climate change scenarios using the SPECIES neural network model. The present European distribution was satisfactorily simulated for 45 species, which showed good statistics of fit between observed species' distributions and derived models. The predicted responses to climate change demonstrate that the distribution of many species in Europe may be affected by climate change, but that the effects are likely to differ between species. The general pattern is of a south-west to north-east shift in suitable climate space, with gains balancing losses for many species. Based on the total change in potential climate space in Europe, the species most sensitive to climate change were *Rubus chamaemorus* (Cloudberry; negatively affected) and *Genista acanthoclada* (Hairy greenweed; positively affected). This disparity in species' response has important implications for EU biodiversity policy as the significance of different countries changes in terms of their future contribution to the conservation of habitats and species.

1. Introduction

Anthropogenic climate change threatens the assumption of static species ranges which underpins current conservation policy. Over the last century, mean annual temperatures have increased by 0.8 °C in Europe, whilst annual precipitation has increased by 10–40% in northern Europe and decreased by up to 20% in parts of southern Europe (Parry, 2000). There is now convincing evidence for a growing human influence on climate (Hulme et al., 2002). The Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2001a) concluded that most of the observed warming over the last 50 years is likely to be attributable to human activities, namely the emission of greenhouse gases. Past and future emissions of greenhouse gases are expected to warm the global climate between 1.4 and 5.8 °C by 2100 (IPCC, 2001a). This projected rate of warming is much larger than the observed changes during the 20th century and is very likely to be without precedent during at least the last 10,000 years, based on palaeoclimate data (IPCC, 2001a).

Evidence is emerging that these changes in climate are already altering some physical and biological systems (IPCC, 2001b). Several studies have shown a link between increases in temperature and an earlier onset of spring conditions (e.g. an advancement in the commencement of leafing and flowering, and the earlier arrival of migrating birds) and a delay in

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autumn conditions (Sparks and Menzel, 2002), as well as changes in plant and animal distributions (e.g. extension of the ranges of birds and butterflies (Thomas and Lennon, 1999; Parmesan et al., 1999)). Meta-analyses encompassing a wide range of taxa by Parmesan and Yohe (2003) and Root et al. (2003) demonstrated that there is a globally coherent fingerprint of climate change impacts on biodiversity. This implies that the projections of future changes in climate proposed by the IPCC in their Third Assessment Report (2001a) are likely to have a substantial impact on natural conservation resources. Current conservation commitments rarely take into account the potential impacts of climate change and quantified scientific evidence is required to support future policy development (Hossell et al., 2003; see Cowling and Pressey, 2003 for a rare exception). For species that have ranges limited by climate, studies that model their responses to projected climate change can inform policy makers about likely shifts in the suitability of regions and help identify those species which are likely to be vulnerable in the future (Harrison et al., 2003; Berry et al., 2006).

At the continental scale, climate is expected to be the dominant factor affecting the distribution of species (Pearson and Dawson, 2003; Thuiller et al., 2004). This implies that studies at the European scale are appropriate for the analysis of climate change impacts on potential species' distributions, as well as being compatible with existing sources of species information (e.g. Jalas and Suominen, 1972–1991). Previous studies on the effects of climate change on species' distributions have often relied on species-climate envelope modelling approaches (Huntley et al., 1995; Sykes et al., 1996; Guisan and Zimmermann, 2000; Thuiller, 2003; Thomas et al., 2004). These approaches use empirical-statistical methods to combine the known current distributions of species with environmental variables to project distributions of species under future climates (see review by Pearson and Dawson, 2003). Different species-climate envelope modelling techniques have been compared and evaluated in several studies. Araújo et al. (2005) report the first independent validation of the four most widely used envelope modelling techniques under climate change (generalized linear models (GLM), generalized additive models (GAM), classification and regression tree analysis (CART) and artificial neural networks (ANN)) using observed distribution shifts among 116 British breeding bird species over the past ~20 years. Thuiller (2003) incorporated the same four modelling techniques in a new computation framework (BIOMOD: BIOdiversity MODelling) for comparing their predictive performance when applied to 61 tree species in Europe. Segurado and Araújo (2004) compared seven modelling techniques for 44 species of amphibians and reptiles in Portugal. All three studies found that no method was superior in all circumstances, but ANNs provided generally more accurate predictions of species range shifts followed by GAMs, then GLMs and CART. This suggests that modelling techniques capable of summarising complex non-linear relationships are more likely to provide useful projections of species responses to climate change (Araújo et al., 2005). In the work described in this paper an existing neural network model (SPECIES, Pearson et al., 2002) has been used to simulate the impacts of climate change on the geographical distribution of 47 plant and animal species across Europe.

The research described in this paper was part of the ACCELERATES project on *Assessing Climate Change Effects on Land Use and Ecosystems: from Regional Analysis to the European Scale*. The ACCELERATES project was undertaken at the scale of the European Union (EU25) plus Romania and Bulgaria, and within six case study regions: Belgium; Denmark; East Anglia, UK; the Belluno Valley, Italy; Almeria, Spain; and the island of Lesvos, Greece. The 47 species modelled at the European scale were chosen to encompass a range of taxa (including plants, insects, birds and mammals) and to reflect dominant and threatened species from habitats that are likely to interact with agricultural land use change, in these six case study regions. Results indicating the potential magnitude and broad pattern of future impacts for these species at the European scale are presented in this paper and implications for European conservation policy discussed. The model presented here has also been downscaled to incorporate finer-scale land cover data and dynamic simulations of species dispersal for a subset of these species at the regional scale. This work was also undertaken as part of the ACCELERATES project and is described in del Barrio et al. (2006). Vulnerability indices combining the sensitivity of the climate space predictions reported here with the adaptation potential of the 47 species are described in Berry et al. (2006) and compared with similar indices of farmer vulnerability related to changes in agricultural land use.

2. Methods

2.1. Data description

Observed species' distributions covering Europe and North Africa were obtained from Hulten (1959), Meusel et al. (1965, 1978, 1992), Jalas and Suominen (1972–1991), Pignatti (1982), Greuter et al. (1984), Daniels and Eddy (1985), Hulten and Fries (1986), Hirit (1999) and Charco (2001) for plants; Willemse (1985), Willense (1995), Kruseman (1988), Minelli et al. (1996) and Tolman (1997) for insects and MacDonald and Barrett (1993) and Mitchell-Jones et al. (1999) for mammals. The European distribution data for birds were supplied electronically through the European Bird Census Council, but can be found in *The EBCC Atlas of European Breeding Birds* (Hagemeijer and Blair, 1997). Additional bird distribution data was obtained from Cramp et al. (1980) and Snow et al. (1998). All distributions were digitised and/or reformatted to a standard 0.5° latitude × 0.5° longitude resolution grid.

Climatic data representing current conditions were required for Europe (34–72°N, 11°W–32°E) and North Africa (15–34°N, 17°W–32°E) for model training and for Europe only for model application. Data for model training was required at a 0.5° spatial resolution to match the observed data on species' distributions, whilst data for model application was available at a 10′ latitude × 10′ longitude resolution. The 10′ dataset was taken directly from New et al. (2001). To ensure consistency between datasets at the different resolutions, the spline surfaces created by New et al. (2001) to produce the 10′ climatology were refitted to a 0.5° elevation grid to create the coarser resolution dataset. Both climatologies contain period-mean monthly observations for the 1961–1990 climatic normal for six surface variables: mean, minimum and maximum temperature, precipitation, cloudiness and mean wind speed. Values of potential evapotranspiration were computed from these climatic variables using the Penman formula (Penman, 1948). Soils data at both resolutions was derived from the IGBP-DIS Global Soil Data Task (2000).

The ACCELERATES climate change scenarios are based on the ATEAM European climate scenarios (Mitchell et al., 2004), but without superimposing the detrended observed (20th century) variability on the modelled (21st century) change fields. Instead, a different measure of inter-annual variability computed from the detrended 1981–1990 average was used for each future 10-yearly time slice. This gives a measure of inter-annual variability without obscuring climate change effects when time slices are compared between themselves and the 1961–1990 baseline. To capture some of the uncertainty surrounding future projections of climate change, scenarios based on two global climate models (HadCM3; Gordon et al., 2000; Pope et al., 2000 and PCM; Washington et al., 2000), two SRES emissions scenarios (A2 and B1; Nakićenović et al., 2000) and three time-slices (2011–2020, 2041–2050 and 2071–2080) were utilised in this study.

The most severe changes in climate occur under the HadCM3 climate model coupled with the A2 SRES scenario. Under this scenario, annual mean temperature averaged over Europe increases by 4.2 °C by 2080. Warming tends to be greatest in southern Europe, with a maximum increase of 7.2 °C and least in northern Europe, where the minimum increase is 1.3 °C. Fairly substantial decreases in precipitation are predicted under this scenario for summer. The European-average decrease is 9.7 mm/month, but much larger decreases of between 30 and 50 mm/month are projected across a band extending from England and France in the west to Romania in the east. In winter, precipitation decreases in southern Europe, but increases everywhere else. The HadCM3 model coupled with the B1 SRES scenario shows a similar pattern of response, but the magnitude is slightly less. The PCM climate model coupled with the A2 SRES scenario shows a different magnitude and pattern of change to both the HadCM3 scenarios. Increases in temperature are generally lower, ranging from 0.4 to 5 °C in summer. For precipitation, projections for summer are generally wetter under the PCM climate model compared with the HadCM3 model, and projections for winter are slightly drier.

2.2. Model description

The SPECIES model (Pearson et al., 2002) was used to characterise the current distribution of selected species in Europe and to estimate their potential re-distribution under alternative climate change scenarios. Forty-seven species associated with 10 habitats that were considered likely to be affected by climate change and agricultural land use change were chosen for the study (Table 1). Species selection was undertaken in conjunction with local stakeholders in the six case study regions of the ACCELERATES project following a protocol to ensure that a range of taxa and dominant and threatened (sensitive/rare) species were modelled. This discussion was facilitated by focus group meetings at the beginning of the project, and bilateral contacts.

Table 1 – Habitats chosen for study by stakeholders in the six ACCELERATES case study regions

Case study	Habitat
Belgium	Acidic beech forest
Denmark	Raised bogs[a], lowland heath
East Anglia, UK	Lowland calcareous grassland[b], cereal field margins[b]
Belluno valley, Italy	Mountain hay meadows[a], siliceous alpine grasslands[a]
Almeria, Spain	Mediterranean arid rangelands
Lesvos, Greece	*S. spinosum* phyrgana[a], mediterranean oak woodland, olive groves

[a] Listed under the Habitats Directive.

[b] UK Biodiversity Action Plan (BAP) priority habitat.

The SPECIES model is based on an artificial neural network, which integrates bioclimatic variables for predicting the distribution of species through the characterisation of bioclimatic envelopes. Integrated algorithms, including a hydrological balance model, are used to pre-process climate (temperature, precipitation, solar radiation, wind speed and potential evapotranspiration) and soils (AWC—available water holding capacity) data to derive relevant bioclimatic variables for input to the neural network. Those variables found to be most successful for bird distributions (Harrison et al., 2003) and other taxa (Berry et al., 2003) are given in Table 2.

The model was trained using existing empirical data on the European and North African (north of 15°N) distributions of species to enable the full climate space of a species to be characterised and to ensure that the model does not extrapolate outside its training dataset when used to predict the distribution of species under potential future climates in Europe. A kriging interpolation function was applied to the observed presence/absence distributions of each species to provide a smoothed suitability surface. The data were then randomly divided into three groups for training, validating and testing the neural network. The validation set ensures that the network does not over-train on the training data, thus losing its ability to generalise, while the test data is used to independently verify the prediction.

Table 2 – Bioclimatic input variables used for birds and other taxa in the SPECIES model

Birds	Other taxa
Growing degree days >5 °C	Growing degree days >5 °C
Absolute minimum temperature expected over a 20-year period	Absolute minimum temperature expected over a 20-year period
Mean summer temperature (MJJ)[a]	Annual maximum temperature
Mean summer precipitation (MJJ)[a]	Accumulated annual soil water deficit
Mean winter precipitation (DJF)[b]	Accumulated annual soil water surplus
Mean summer water availability (MJJ)[a]	

[a] May–July.

[b] December–February.

The performance of each network was statistically analysed using Cohen's kappa statistic of similarity (κ) and the area under the receiver operating characteristic curve (AUC). κ is a commonly used statistic that provides a measure of proportional accuracy, adjusted for chance agreement (Cohen, 1960). κ varies from 0, indicating no agreement between observed and predicted distributions, to 1 for perfect agreement. AUC is an unbiased measure of prediction accuracy calculated from the receiver operating characteristic (ROC) curve (Fielding and Bell, 1997). The ROC curve describes the compromise that is made between the sensitivity (defined as the proportion of true positive predictions versus the number of actual positive sites) and false positive fraction (the proportion of false positive predictions versus the number of actual negative sites). This index is independent of both species prevalence and the decision threshold for defining species' suitability. AUC ranges from 0.5 for models with no discrimination ability, to 1 for models with perfect discrimination.

The SPECIES results show areas of maximum potentially suitable climate space and various factors will prevent the realisation of this (Berry et al., 2003; Harrison et al., 2003). In particular, many species display strong associations with specific habitat types. Habitat was not included in training the SPECIES model because consistent datasets do not exist for the wider European region. It is therefore likely that the model may predict the presence of a species in an area where there is no suitable habitat at present. Further, the presence of species may depend on their tendency to disperse or migrate. It was not possible to run a dynamic dispersal model at the continental scale to assess the ability of species to track changes in their potential climate space due to data and computer run-time limitations. These limitations to the predictive capacity of species-climate envelope modelling approaches (along with others) are discussed in more detail later. However, they imply that the predictions should be interpreted with due caution and should be viewed as first approximations indicating the potential magnitude and broad pattern of future impacts, rather than as accurate simulations of future species' distributions.

3. Results

3.1. Model validation

Table 3 summarises the statistical performance of the SPECIES model at replicating the observed European species' distributions. The AUC statistic was >0.9 for 42 of the 47 species, indicating very good discrimination ability (Swets, 1988). Three species had values between 0.7 and 0.9 indicating reasonable discrimination, whilst two species had values below 0.7 showing poor discrimination ability. The κ statistic is slightly lower for most species as the index ranges between 0 and 1. Here, 38 species show values >0.7, indicating very good agreement between observed and simulated distributions, seven species show a value between 0.4 and 0.7 indicating reasonable agreement, and two species show values of <0.4 indicating poor agreement (Monserud and Leemans, 1992).

Table 3 – Independent testing of the European-scale neural network SPECIES models using the area under the receiver operating characteristic curve (AUC) and Cohen's kappa statistic of similarity (κ)

Species	AUC	κ
Acidic beech forest		
Fagus sylvatica	0.810	0.795
Ciconia nigra[a]	0.961	0.719
Luzula sylvatica	0.974	0.763
Ficedula hypoleuca[a]	0.999	0.884
Vaccinium myrtillus	0.987	0.903
Sorbus aucuparia	0.988	0.922
Anthus trivialis[a]	0.984	0.905
Picus canus[a]	0.972	0.830
Raised bogs		
Rubus chamaemorus	0.980	0.863
Sphagnum cuspidatum	0.963	0.747
Molinia caerulea	0.986	0.912
Grus grus[a]	0.984	0.872
Lowland heath		
Ulex europaeus	0.986	0.827
Genista pilosa	0.956	0.692
Empetrum nigrum	0.971	0.796
Arctostaphylos uva-ursi	0.972	0.798
Lowland calcareous grassland		
Hesperia comma[b]	0.959	0.875
Campanula glomerata	0.985	0.861
Helictotrichon pratense	0.960	0.757
Lysandra bellargus[b]	0.988	0.877
Cereal field margins		
Silene gallica	0.943	0.640
Papaver dubium	0.971	0.853
Legousia hybrida	0.983	0.871
Lepus europaeus[c]	0.985	0.893
Mountain hay meadows/Siliceous alpine grassland		
Arrhenatherum elatius	0.704	0.847
Chorthippus dorsatus Dorsatus[b]	0.788	0.857
Alopecurus pratensis	0.988	0.904
Gymnadenia conopsea	0.977	0.872
Crex crex[a]	0.971	0.786
Microtus arvalis[c]	0.971	0.856
Ostrya carpinofolia	0.971	0.587
Capreolus capreolus[c]	0.982	0.868
Mediterranean arid rangelands		
Quercus ilex	0.994	0.869
Chamaerops humilis	0.968	0.694
Pinus pinaster	0.931	0.492
Pinus halepensis	0.957	0.508
Quercus faginea	0.978	0.635
Pistacia lentiscus	0.973	0.798
Nerium oleander	0.510	0.789
Sarcopoterium spinosum phyrgana		
Sarcopoterium spinosum	0.993	0.863
Genista acanthoclada	0.146	0.010
Vulpes vulpes[c]	0.991	0.927
Mediterranean oak woodland		
Quercus macrolepsis	0.973	0.367
Dendrocops medius[a]	0.980	0.809
Olive groves		
Olea europea	0.982	0.822
Matricaria chamomilla	0.979	0.838
Sciurus anomalus[c]	0.982	0.908

[a] Bird.
[b] Insect.
[c] Mammal.

3.2. *Model application*

The SPECIES model was used to simulate the potential climate space of 47 species across Europe and results are summarised in Table 4 for all three time-slices from the HadCM3 A2 and PCM A2 scenarios. Results for the HadCM3 B1 scenario tend to fall in between those shown for the HadCM3 A2 and PCM A2 scenarios.

3.2.1. *Belgian selected habitat and species*

The dominant species of the acidic beech woodland (*Fagus sylvatica*: Beech) gains more climate space in the UK and Scandinavia than it loses in southern Europe. In contrast, several other species (e.g. *Ficedula hypoleuca*: Pied flycatcher; *Vaccinium myrtillus*: Bilberry; *Sorbus aucuparia*: Rowan and *Anthus trivialis*: Tree pipit) lose more climate space than they gain, implying that the understorey and ground floor composition of this habitat could alter. *V. myrtillus* and *S. aucuparia* do not show any gain at all under most of the scenarios, only *S. aucuparia* gains 1% under the PCM A2 2080 scenario. These species all lose space initially right across southern Europe, and increasingly through central and eastern Europe over time, *V. myrtillus* to the extent where the only suitable climate space under the HadCM3 A2 2080 scenario outside Scandinavia and the UK is across the Swiss Alps, north-west France, Belgium and the Netherlands, and in patches in the Balkans and Germany. These species all maintain space in Scandinavia, *A. trivialis* showing gains here with time. The other three species (*Ciconia nigra*: Black stork; *Luzula sylvatica*: Great woodrush and *Picus canus*: Grey-headed woodpecker) show the same general trend as *F. sylvatica* with increasing losses across southern and western Europe, but statistically greater gains in Scandinavia, *C. nigra* gaining the most climate space (66% under the HadCM3 A2 scenario).

3.2.2. *Danish selected habitats and species*

Raised bogs are important for conservation, being listed under the Habitats Directive and are particularly sensitive to climate change—their hydrological requirements are very precise and their component species are primarily specialists lacking the ability to adapt to changed conditions. All four raised bog species lose more climate space than they gain under all the scenarios, with *Rubus chamaemorus* (Cloudberry) and *Molinia caerulea* (Purple moor grass) showing no overall increase in suitable space and *Sphagnum cuspidatum* (a bog moss) and *Grus grus* (Common crane) only small gains across northern Scandinavia. The species all show a retraction of their climate space over time, initially from the south and south-west, and increasingly through central and western Europe under all scenarios, most extremely under the HadCM3 A2 scenario. *G. grus* and *R. chamaemorus* become largely confined to Scandinavia but not Denmark, except under the PCM A2 2020 and 2050 scenarios for *G. grus*. Climate, however, is not the only factor determining species' distributions and currently *G. grus* populations are increasing in Denmark, possibly through reduced hunting pressure (Kurt Rasmussen, personal communication).

The dominant lowland heath species (*Ulex europaeus*: Gorse and *Genista pilosa*: Hairy greenweed) remain relatively stable in terms of overall geographical range. However, the others (*Empetrum nigrum*: Crowberry and *Arctostaphylos uva-ursi*: Bearberry) lose a large proportion of suitable climate space, particularly under the HadCM3 A2 and B1 scenarios, and only gain a little in northern Scandinavia. As with the raised bog species, the general trend is of initial loss of climate space from the south and south-west of Europe, and increasingly with time from central and eastern Europe.

3.2.3. *UK selected habitats and species*

Lowland calcareous grasslands are largely restricted to the warmer and drier climates of the southern and eastern areas of the United Kingdom and are a Biodiversity Action Plan (BAP) priority habitat, partly due to a decline in habitat quantity and fragmentation, as well as loss of quality (e.g. through agricultural intensification). All four lowland calcareous grassland species show a south-west to north-east shift in suitable climate space under all scenarios, with increasing suitability across the UK and Scandinavia, and loss of space from southern Europe. For the two butterfly species, *Hesperia comma* (Silver-spotted skipper) and *Lysandra bellargus* (Adonis blue), both BAP species, and *Campanula glomerata* (Clustered bellflower), this shift is greater under the HadCM3 A2 and B1 scenarios than under the PCM A2 scenario. *Helictotrichon pratense* (Meadow oat-grass), however, gains more space under the PCM A2 scenario, while losing more space under both HadCM3 scenarios. Although there may be new climate space for all the modelled lowland calcareous grassland species, available calcareous strata will be more restricted.

Cereal field margins are a BAP Priority habitat because changes in cropping patterns and practices have led to reductions in habitat extent. The cereal field margin species, *Silene gallica* (small-flowered catchfly) and *Papaver dubium* (long-headed poppy), lose more climate space than they gain under the HadCM3 A2 and B1 scenarios, leading to an overall loss of 39% and 28%, respectively, by 2080. However, the opposite situation is predicted under the PCM A2 scenario, namely they gain more suitable space than is lost, leading to an overall gain in climate space of 21% and 2%, respectively (Fig. 1). This highlights the importance of including more than one scenario to capture some of the range of uncertainty in future projections of climate change. Both species show a general retraction of climate space across much of southern and eastern Europe, only gaining some ground in the UK and southern Scandinavia. *Legousia hybrida* (Venus's-looking-glass) and *Lepus europaeus* (Brown hare) lose only a little climate space, except for *L. europaeus* under the HadCM3 A2 2080 scenario where 18% of baseline suitability is lost across Spain, Italy, Greece, southern France and the UK. Gains in climate space are large for both species, particularly *L. hybrida* which expands into central and north-eastern Europe and parts of Scandinavia.

3.2.4. *Italian selected habitats and species*

The Italian selected habitats, mountain hay meadows/siliceous alpine grassland, are listed under the Habitats Directive and all the modelled species show a very similar pattern in the response of their suitable space to climate change. This is a general but gradual shift along the south-west to north-east axis under all the scenarios, losing most space in central Europe under the HadCM3 A2 scenario. *Alopecurus pratensis*

Table 4 – Gains (+) and losses (−) in European climate space (%) simulated by the SPECIES model under two scenarios

Species	HadCM3 A2 scenario			PCM A2 scenario		
	2020	2050	2080	2020	2050	2080
UK						
Hesperia comma[b]	+7/−3	+13/−4	+23/−7	+5/−3	+9/−3	+19/−6
Campanula glomerata	+13/−8	+21/−16	+26/−29	+7/−6	+13/−10	+22/−16
Helictotrichon pratense	+22/−18	+28/−28	+32/−50	+23/−10	+30/−17	+43/−26
Lysandra bellargus[b]	+21/−9	+29/−21	+40/−43	+16/−5	+23/−10	+31/−18
Silene gallica	+22/−25	+23/−44	+25/−64	+23/−16	+35/−23	+54/−33
Papaver dubium	+6/−19	+7/−29	+12/−40	+9/−12	+13/−14	+20/−18
Legousia hybrida	+38/−1	+53/−2	+66/−3	+25/−1	+34/−2	+56/−3
Lepus europaeusc[c]	+10/−2	+16/−5	+24/−18	+7/−2	+10/−3	+17/−6
Belgium						
Fagus sylvatica	+30/−10	+39/−18	+53/−31	+26/−7	+36/−10	+49/−15
Ciconia nigraa[a]	+30/−26	+45/−35	+66/−45	+30/−25	+42/−29	+56/−37
Luzula sylvatica	+31/−15	+38/−27	+46/−47	+28/−9	+40/−15	+56/−22
Ficedula hypoleuca[a]	+3/−16	+4/−38	+4/−56	+2/−8	+2/−16	+2/−33
Vaccinium myrtillus	+0/−12	+0/−29	+0/−52	+0/−6	+0/−12	+0/−22
Sorbus aucuparia	+0/−8	+0/−17	+0/−33	+0/−5	+0/−7	+1/−13
Anthus trivialisa[a]	+2/−9	+3/−17	+3/−36	+1/−6	+2/−9	+3/−14
Picus canusa[a]	+11/−8	+22/−11	+34/−13	+7/−6	+15/−7	+30/−7
Denmark						
Rubus chamaemorus	+0/−34	+0/−47	+0/−68	+0/−22	+0/−39	+0/−53
Sphagnum cuspidatum	+8/−35	+14/−51	+13/−69	+6/−21	+14/−29	+19/−37
Molinia caerulea	+0/−10	+0/−19	+0/−33	+0/−6	+0/−10	+0/−15
Grus grusa[a]	+9/−23	+9/−44	+8/−61	+9/−17	+8/−33	+6/−59
Ulex europaeus	+13/−14	+17/−24	+20/−41	+14/−9	+21/−13	+34/−19
Genista pilosa	+33/−23	+42/−42	+44/−69	+29/−14	+41/−22	+61/−36
Empetrum nigrum	+2/−35	+3/−51	+6/−64	+2/−21	+3/−32	+5/−43
Arctostaphylos uva-ursi	+53/−76	+14/−45	+3/−58	+2/−16	+4/−28	+4/−39
Italy						
Arrhenatherum elatius	+6/−14	+12/−22	+24/−35	+6/−10	+11/−13	+20/−16
Chorthippus dorsatus dorsatus[b]	+13/−12	+23/−29	+37/−60	+8/−6	+13/−13	+23/−24
Alopecurus pratensis	+1/−11	+1/−23	+2/−46	+1/−6	+1/−11	+1/−22
Gymnadenia conopsea	+1/−12	+3/−24	+3/−43	+2/−7	+3/−10	+3/−18
Crex crexa[a]	+8/−14	+15/−35	+18/−76	+6/−10	+11/−17	+21/−31
Microtus arvalis[c]	+14/−7	+24/−18	+36/−40	+8/−3	+15/−7	+25/−17
Ostrya carpinofolia	+78/−21	+114/−38	+143/−58	+57/−14	+33/−23	+116/−35
Capreolus capreolus[c]	+2/−9	+3/−20	+4/−39	+1/−5	+2/−9	+3/−16
Spain						
Quercus ilex	+17/−5	+34/−9	+69/−15	+10/−3	+20/−3	+37/−6
Chamaerops humilis	+29/−7	+60/−7	+106/−12	+18/−6	+34/−4	+60/−3
Pinus pinaster	+23/−18	+33/−33	+57/−52	+20/−10	+26/−14	+34/−27
Pinus halepensis	+37/−1	+80/−4	+158/−11	+20/−1	+41/−2	+72/−4
Quercus faginea	+38/−5	+66/−9	+120/−24	+27/−4	+37/−4	+49/−6
Pistacia lentiscus	+53/−0	+113/−1	+190/−12	+36/−0	+58/−0	+115/−0
Nerium oleander	+50/−0	+115/−0	+210/−1	+33/−0	+51/−0	+94/−0
Greece						
Sarcopoterium spinosum	+106/−3	+164/−15	+198/−48	+74/−2	+108/−6	+155/−18
Genista acanthoclada	+103/−8	+177/−14	+386/−31	+61/−8	+103/−10	+160/−19
Vulpes vulpes[c]	+1/−1	+1/−1	+2/−1	+1/−1	+1/−1	+1/−1
Quercus macrolepsis	+67/−22	+197/−34	+373/−61	+34/−21	+76/−26	+162/−38
Dendrocops medius[a]	+27/−8	+41/−18	+56/−39	+22/−6	+36/−9	+53/−16
Olea europea	+24/−4	+46/−8	+104/−11	+14/−2	+27/−2	+45/−2
Matricaria chamomilla	+8/−11	+15/−19	+23/−29	+6/−7	+10/−11	+19/−17
Sciurus anomalus[c]	+3/−11	+4/−20	+5/−30	+2/−7	+3/−12	+5/−19

[a] Bird.
[b] Insect.
[c] Mammal.

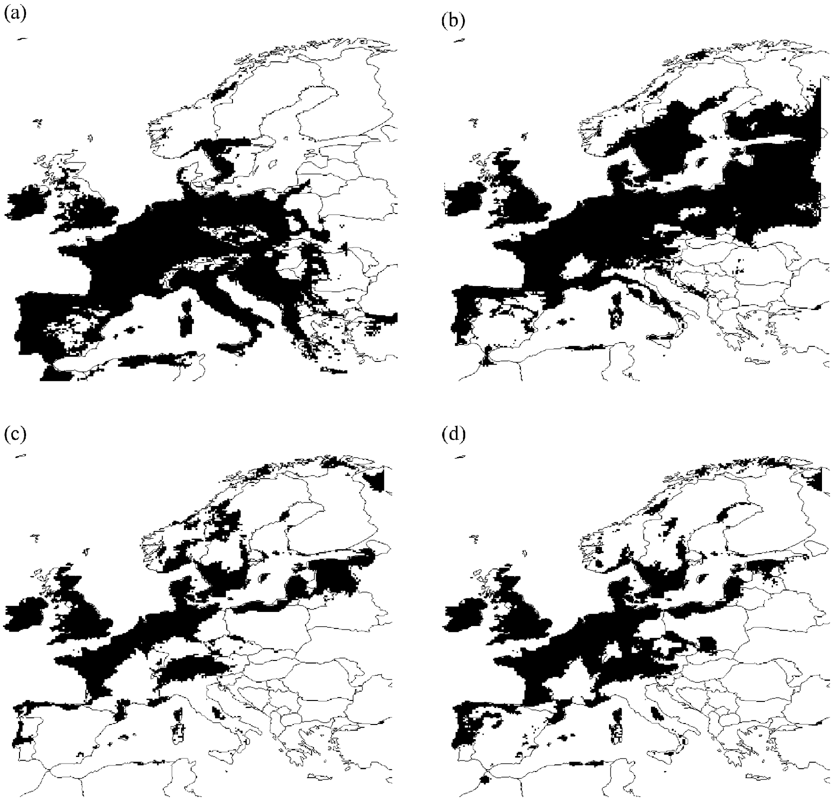

Fig. 1 – Simulated climate space for *S. gallica*: (a) baseline (1961–1990); (b) PCM A2 2080 scenario; (c) HadCM3 A2 2080 scenario and (d) HadCM3 B1 2080 scenario.

(Meadow foxtail), *Gymnadenia conopsea* (Fragrant orchid) and *Capreolus capreolus* (Roe deer) show virtually no gain in climate space, whilst *Arrhenatherum elatius* (False oat-grass), *Chorthippus dorsatus dorsatus* (Steppe grasshopper), *Crex crex* (Corncrake) and *Microtus arvalis* (Common vole) show a moderate expansion in climate space into the UK and Scandinavia. At the European scale, *C. crex* (a globally threatened species) is the most sensitive of all the species modelled, especially after 2050, losing between 35% and 76% of climate space from all of southern, and most of central and western, Europe under the HadCM3 A2 scenario (Fig. 2). It is also highly vulnerable in Italy, as only isolated high mountain areas remain climatically suitable by 2080. *Ostrya carpinofolia* (Hop hornbeam), on the other hand, shows the most gain under the scenarios, with a substantial increase in climate space through central, eastern and northern Europe of up to 143% relative to the baseline.

3.2.5. *Spanish selected habitats and species*

Of the Mediterranean arid rangeland species, *Pistacia lentiscus* (Mastic tree) and *Nerium oleander* (Oleander) lose virtually no climate space and gain the most space of the Spanish case study species, generally spreading north and west right across their ranges, especially under the HadCM3 A2 scenario (190% and 210% gain by 2080, respectively). *Pinus halepensis* (Aleppo pine) and *Quercus faginea* (Portuguese oak) show a similar pattern, but to a lesser degree, and with some loss of space in southern Spain under both the HadCM3 A2 and B1 scenarios. *Chamaerops humilis* (European fan palm) and *Quercus ilex* (Holm oak) gain space to the north and north-east, while losing some space in the south-east of their ranges. Thus, many of the Mediterranean rangeland species appear to be less vulnerable to climate change at the European scale than those modelled from other countries, except perhaps some from Greece, as there is an expansion in suitable climate space northwards, without large losses in the south (Berry et al., 2006). The exception is *Pinus pinaster* (Maritime pine) for which much of Spain becomes unsuitable by 2080 under the HadCM3 A2 and B1 scenarios.

3.2.6. *Greek selected habitats and species*

Of the Greek selected habitats, *Sarcopoterium spinosum* phyrgana is listed under the Habitats Directive and of the species selected for this habitat, *Vulpes vulpes* (Red fox) shows virtually no change in its climate space under all scenarios, and both *Genista acanthoclada* (Spiny broom) and *S. spinosum* (Thorny burnet) show large increases in their climate range (386% and 198% under the HadCM3 A2 2080 scenario), spreading from the south-east through central and northern Europe and across to western France and Spain, and for *S. spinosum*, further north into Scandinavia. Of the Mediterranean oak woodland species, *Quercus macrolepsis* (Valonia oak) follows a very similar pattern, increasing especially through the Balkans and France, while *Dendrocops medius* (Middle-spotted woodpecker) shows a retraction in its central European climate space with a spread northwards into Scandinavia, most markedly under the HadCM3 A2 scenario. *Olea europea* (Olive) gains the most space of the olive grove species, increasing to the west and north-west of its range. *Matricaria chamomilla* (Chamomile) and

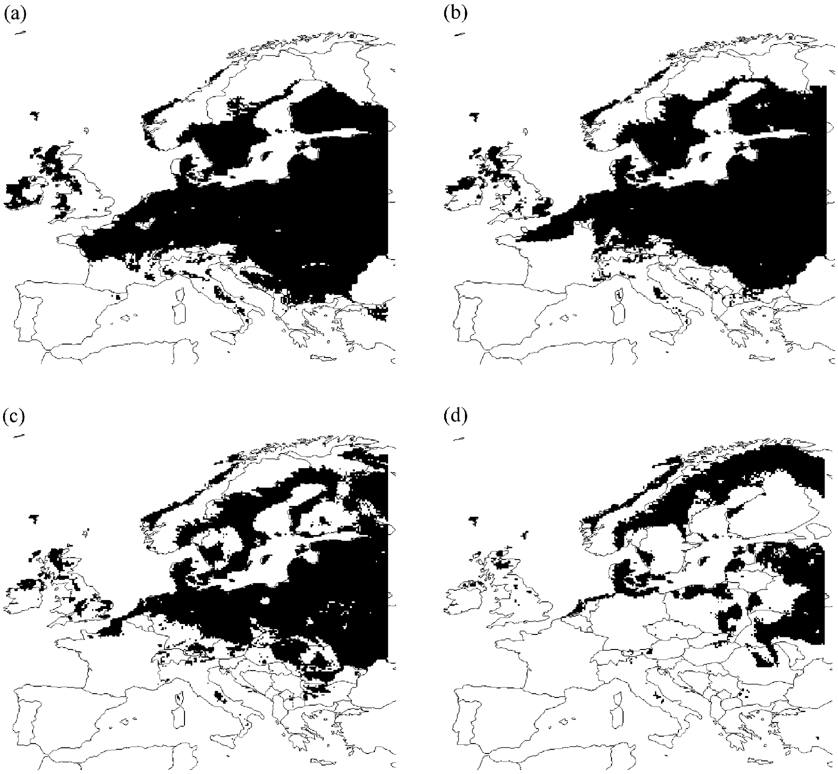

Fig. 2 – Simulated climate space for *C. crex*: (a) baseline (1961–1990); (b) HadCM3 A2 2020 scenario; (c) HadCM3 A2 2050 scenario and (d) HadCM3 A2 2080 scenario.

Sciurus anomalus (Persian squirrel) both lose space from the west and south-west, with suitable space for *S. anomalus* across central Europe becoming increasingly fragmented, while *M. chamomilla* gains space further north into Scandinavia. Three species experience significant reductions in potential climate space within Greece: *M. chamomilla*, *S. anomalus* and *Q. macrolepsis* losing 88%, 98% and 56%, respectively under the HadCM3 A2 2080 scenario. However, these species are not particularly vulnerable at the European scale and thus this is a national issue (Berry et al., 2006).

The general pattern is of a south-west to north-east shift, which corresponds with the findings of other research, e.g. Huntley et al. (1995), Sykes and Prentice (1995), Harrison et al. (2001), Hill et al. (2003), and Skov and Svenning (2004). Very broadly, the southern European species gain the most space, and the northern European ones lose the most, partly due to limited unoccupied space in the north. The results show that there is a variable response between habitats and countries, dependent on the location and range size of their component species. Only a small sample of species was modelled for each habitat and thus they may not be representative of the overall habitat response, but the responses of dominants may be indicative of the habitat's future. This disparity in species' response has important implications for EU biodiversity policy as the significance of different countries changes in terms of their future contribution to the conservation of habitats and species.

The results need to be treated with a certain degree of caution as the models only simulate potential future distribution and ideally they need validating either by hindcasting or by long-term future monitoring. Nevertheless, given the consistent trend of species response, both within this study and across other studies, the results can be useful for guiding the development of future conservation policy at the European scale.

4. Policy implications

The EU is committed to biodiversity conservation e.g. through the Convention on Biological Diversity and its own target to halt the loss of biodiversity by 2010 (and to sustain it thereafter). The EU has two key relevant conservation measures—the *Birds* and *Habitats* directives. The *Birds* directive is concerned with the long-term protection and management of all wild birds, especially migratory species, and their habitat. Rare and endangered birds have special conservation measures. Member states must classify the most appropriate areas as special protection areas (SPA). The *Habitats* directive is the main means of safeguarding biodiversity, whereby member states are obliged to protect species and habitats of interest to the community. Each member state is responsible for identifying and designating as special areas of conservation (SAC), sites which are important for species and habitats listed in the directive. These sites benefit from statutory or contractual measures and, where appropriate, management plans which will ensure their long-term preservation by integrating human activities into a sustainable development strategy.

EU policy is targeted at meeting its commitment to the international Convention on Biological Diversity. This is being done through the establishment of a Natura 2000 network of designated sites, based on SPAs and SACs, and the European Community Biodiversity Strategy. These sites are seen as the cornerstone of EU nature protection policy and the network already comprises more than 18,000 sites, covering over 17% of EU territory. The purpose of the network is not to create nature reserves where all human activity will be systematically excluded, but to provide an opportunity to demonstrate how conservation can be integrated into other policies, including those relating to land use (see Berry et al., 2006). The European Community Biodiversity Strategy aims for the conservation and sustainable use of biological and landscape diversity in its regions within 20 years. A Pan-European Ecological Network is planned to be realised by 2005, along which animal and plant species would be able to migrate freely. It is both a physical network through which ecosystems, habitats, species, landscapes and other natural features of European importance are conserved, and a coordinating mechanism through which the partners in the Strategy can develop and implement cooperative actions. It will build on a variety of existing initiatives, including Natura 2000, the European network of Biogenetic Reserves, the EECONET concept, the Bern Convention, the Bonn Convention, and the many national and regional ecological networks already under development.

These international and EU-level policies and Directives concern aspects of the environment on which climate change will have an effect and, increasingly, the importance of taking climate change into account is being recognised. The Malahide Conference in 2004, for example, had as part of one of its objectives that the habitats and species most at risk from climate change should be assessed by 2007, and appropriate management plans subsequently prepared. These policies and objectives will require implementation (and perhaps revision, in due course) that is sensitive to climate change and must be based on a surer knowledge of the vulnerability of their valued environmental components to such change. The results from the SPECIES model have indicated that climate change will lead to alterations in the suitable climate space for species, with some species benefiting and others with reduced potential future distributions. These have important implications for conservation policy through changing species' vulnerability, with consequences for the habitats they represent (Berry et al., 2006).

The Habitats Directive states that the conservation of a natural habitat will be taken as favourable when its natural range, and areas it covers within that range, are stable or increasing, and the specific structure and functions which are necessary for its long-term maintenance exist and are likely to continue to exist for the foreseeable future. Many of the selected habitats (see Table 1) are listed under the EU Habitats Directive (e.g. *S. spinosa* phrygana, siliceous alpine grassland and montane hay meadows), while others are of national importance (e.g. lowland calcareous grassland). All the species modelled for siliceous alpine grassland and montane hay meadows lost significant proportions of their current climate space and thus the ability to maintain the species and habitat in favourable conservation status could be severely compromised by climate change. Species which are losing suitable climate space are more likely to be in equilibrium with their contracting climate space, but populations may be able to persist in microhabitats, for example, mountain hay meadow species on north-facing slopes. There is probably little that can be done climatically for many of these species, unless suitable microclimates for certain species can be created through the management of vegetation height. Other management options include reducing any known additional stresses, such as grazing pressure or scrub invasion. Local losses are less significant providing the species has adequate climate space elsewhere, but may be of concern where it is an important component of a habitat, such as *S. cuspidatum* (Danish raised bogs) and the grasses: *A. elata* and *A. pratensis* in siliceous alpine grassland and montane hay meadows.

None of the modelled species are listed under the EU Habitats Directive, but six of the birds (*C. nigra*, *F. hypoleuca*, *P. canus*, *C. crex*, *G. grus* and *D. medius*) are listed in the Birds Directive. As many of the plant species were chosen as characteristic of habitats, often they are dominants and widespread, not vulnerable to climate change, and although rarer species are potentially threatened by climate change, none of the above are highly vulnerable at the European scale in terms of range reduction and lack of overlap between their current and potential future distribution. Three of the birds (*F. hypoleuca*, *C. crex* and *G. grus*) show an overall loss in climate space at the European scale under all the scenarios. *G. grus* (Denmark) loses all suitable climate space and *C. crex* (Italy) loses over 90% by 2080 under all scenarios. The conservation status for species is considered to be 'favourable' when population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats and the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future. In the case of *G. grus* and *C. crex*, high priority needs to be given to its conservation in its areas of remaining suitable climate space and if it is not already of favourable conservation status here then restoration is of the utmost urgency.

The possibility of a species expanding its range into new potential climate space depends on its dispersal ability and the role of long-distance dispersal. Species have variable dispersal ability and most plant species are unlikely, in the time-scale under consideration, to be able to fulfil their total new potential climate space where this represents an increase in their range northwards, even if long-distance dispersal occurs. Other taxa may have greater dispersal ability. Most butterflies disperse short distances, although it is possible that individuals may be blown longer distances, but their survival then depends on them finding a suitable habitat. Much species' movement will be across managed land and here more environmentally friendly management techniques, at least in selected areas, could be helpful, e.g. minimising spraying adjacent to verges, banks and hedges and leaving small areas of unmanaged land. The new Common Agricultural Policy will help to achieve this by transforming the farmer from a producer of food to a guardian of nature through a redirection of public subsidies from pure production to a greater range of ecosystem services, including the protection, preservation and improvement in the abundance of biodiversity.

At the national scale, many of the modelled species are highly sensitive to climate change. For these species, a long-term commitment to monitoring may be required to verify such predictions and conservation management and legislation may need strengthening in order to maintain them. Increasing the size of habitat by expanding designated/protected areas (e.g. Natura 2000 sites) will help in the continuance of a species in a particular location, with a focus perhaps on reserves towards or immediately beyond the northern or north-eastern edge of the species' current range. The effectiveness of corridors is unproven for most species, but trying to minimise large east-west barriers is helpful. Translocation is another method for reducing vulnerability, but it is dependent on suitable new habitat being available and care needs to be taken that the species does not become a problem in its new environment. Given the number of species possibly needing assistance in adapting to climate change, this is unlikely to be feasible except in a few cases, and for northern species habitat availability will be a serious issue.

It also raises the important policy issues of whether new species arriving in an area are going to be classified as aliens, especially if native within a country and how the potential for invasion is going to be monitored and managed. This kind of non-equilibrium situation will test the abilities of conservation managers to manage their ecosystems with established skill-sets. New policies and codes of practice will be needed, and transnational co-ordination and co-operation will be particularly important.

The work presented in this paper from the ACCELERATES project can contribute to meeting some objectives of the Malahide conference by identifying both habitats and species at risk from climate change and agricultural areas at risk from biodiversity loss. Results from the SPECIES model indicate that the ability of countries to meet the requirements of the EU Directives may be compromised by climate change, and that a more dynamic, holistic, international strategy for conservation is critical for sustaining biodiversity in the context of climate change.

5. Discussion and conclusions

The great complexity of natural systems suggests that there are fundamental limits to the accurate prediction of future species' distributions (Pearson and Dawson, 2003). The species-climate envelope approach used in the SPECIES model is valuable as it allows an objective description of the potential climate space of species across Europe and can provide a tentative first approximation of the impacts of climate change for guiding monitoring and experimental programs, which can test the limits identified by the models (Harrison et al., 2003). The benefits and limitations of neural networks compared to other species-climate envelope modelling techniques are discussed in Pearson and Dawson (2003), and have been evaluated in Huntley et al. (2004), Segurado and Araújo (2004), Thuiller (2003) and Araújo et al. (2005). Such approaches do not take into account possible physiological effects of changes in climate or atmospheric CO_2 on species, but they do allow a large selection of species to be modelled for which detailed ecophysiological data may not be available (Harrison et al., 2003). This species-climate envelope approach is most useful for continental scale studies where climate is expected to be the dominant factor affecting species' distribution (Berry et al., 2002; Pearson and Dawson, 2003; Huntley et al., 2004; Thuiller et al., 2004). The ability of the model to train on the basis of climate alone is reflected in the high measure of agreement between the observed and simulated distributions.

However, there are important limitations to the predictive capacity of species-climate envelope models which should be heeded when interpreting the model results. It has already been mentioned that habitat and dispersal ability were not included in the SPECIES model due to data limitations. It is therefore likely that the model may predict the presence of a species in an area where there is no suitable habitat or the likelihood of a species colonising a new area may be reduced if situated a long distance from its current range. These limitations to modelling at the continental scale have been addressed within the ACCELERATES project at the regional scale and results are described in del Barrio et al. (2006). The SPECIES modelling approach has been extended to include land cover variables in a second neural network within the regional case studies where such datasets are available. Further, a dispersal model has been integrated with the predictions of species' distributions at this regional scale to assess the ability of species to track changes in their potential climate space.

The population dynamics of a species will also influence how its distribution tracks changes in its potential climate space. If a species is in decline it may not necessarily expand its range in response to an increase in its area of climatic suitability. Improving climatic conditions may slow the rate of decline but may not necessarily halt or reverse it. Similarly, a reduction in potential climate space may cause a disproportionate decrease in an already declining species (Harrison et al., 2003).

The species-climate envelope modelling procedure is based on the assumption that current species distributions are in equilibrium with the current climate and that the relationship between species and climatic factors will remain fixed (Harrison et al., 2003). It is possible, however, that species will adapt to changing climatic conditions and may still be responding to earlier changes in climate or CO_2 concentration. Predicting autonomous adaptive changes to species in response to climate change has not been accounted for within the SPECIES model, which could lead to changes in the levels of parameters describing their potential climate space. Thus, model results are likely to be most appropriate for species not expected to be able to undergo rapid evolutionary change over the next century (Pearson and Dawson, 2003).

Finally, the importance of biotic interactions between species, such as competition, predation and symbiosis with other species, have been shown to have important impacts on species distributions (Silander and Antonovics, 1982; Davis et al., 1998). Changes to the distribution of a single species could have significant knock-on impacts on the distributions of many other species. Thus, modelling strategies based on species-climate envelopes alone may in some cases lead to predicted distributions that are erroneous. However, Pearson and Dawson (2003) argue that applying bioclimatic models at macro-scales, where climatic influences on species distributions are shown to be dominant, minimises the impact of biotic interactions.

Further research is needed to explore the relationships between climate change and associated changes in habitats, biotic interactions and species' adaptive capacity so that we can have a better understanding of the consequences it may have for species' distributions. The outputs of the SPECIES model show that species whose southern range margins are in Europe, such as *S. aucuparia* and *G. pilosa*, will progressively lose suitable climate space. Alternatively, species that have their northern range margins in Europe or have a restricted southern European distribution, such as *N. oleander* and *C. humilis*, will have the potential to expand. The consequences of climate change for the different habitats are, therefore, variable. Where the trend for component species is consistent, as is the case for the mountain hay meadows in Italy and Mediterranean arid rangelands in Spain, then it could be assumed that they would retract or expand their range respectively. This assumption is based on other component species showing a similar response. Elsewhere, the future of the habitat appears to depend much more on the species under consideration. If the dominants continue to find suitable climate space, as is the case in acidic beech woodlands, then it could be assumed that the habitat would continue in existence, but with a slightly different species composition. Other habitats, such as cereal field margins and lowland calcareous grassland in the UK, however, show a mixed response between species and scenarios. In these cases, additional modelling of a wider range of species and climate change scenarios would help to test the above assumptions.

An alternative approach to identifying habitat change is more mechanistic, dynamic global vegetation models (DGVM). They have the advantage of being process based, but generally operate at a coarser scale. They also have a limited range of plant functional types, which often do not match well the habitats of interest to conservation managers and policy-makers, especially at the continental to regional scale.

Given such a dynamic future for both individual species and their associated habitats, it is important that appropriate measures are taken, where possible, in order to safeguard vulnerable species and to facilitate the movement of others. The predicted responses to climate change differ between species, but there is a general south-west to north-east shift in suitable climate space, with gains balancing losses for many species. Thus, the significance of different countries in terms of their future contribution to the conservation of habitats and species is likely to change in the future, with countries in Scandinavia and northern continental Europe becoming increasingly important. This trans-national nature of conservation under climate change will require EU policy strategies that are more dynamic and holistic, and which are regularly reviewed and updated as scientific knowledge is advanced.

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