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Integrating multiple modelling approaches to predict the potential impacts of climate change on species' distributions in contrasting regions: comparison and implications for policy

G. del Barrio^{a,*}, P.A. Harrison^b, P.M. Berry^b, N. Butt^b, M.E. Sanjuan^a,
R.G. Pearson^c, T. Dawson^d

^a Estacion Experimental de Zonas Aridas (CSIC), General Segura 1, 04001 Almeria, Spain

^b Environmental Change Institute, Oxford University Centre for the Environment, Dyson Perrins Building, South Parks Road, Oxford, OX1 3QY, UK

^c Department of Herpetology & Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

^d Centre for the Study of Environmental Change and Sustainability, University of Edinburgh, The King's Buildings, West Mains Road, Edinburgh EH9 3JN, UK

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ABSTRACT

Many studies have predicted the potential impacts of climate change on species' distributions at large spatial scales, yet the role of more local-scale effects remains poorly explored. Addressing more localised impacts requires that new integrated modelling approaches are developed to address fine-scale processes including species' dispersal and local connectivity. Here we integrate four models (a continental scale bioclimatic envelope model, a regional scale bioclimate and land use suitability model, a dispersal model, and a connectivity model) in a scale-dependent hierarchical framework. The approach has been used to analyse the fine scale impacts of climate change on species' distributions within two contrasting case study regions located in East Anglia (UK) and Almeria (Spain). Eight and six species respectively were used to test our approach under three climate change scenarios. Despite the uncertainties inherent in the modelling approach, our analyses suggest two general conclusions: (i) climate change involves the development of transient conditions and fragmentation within the core of species distributions; (ii) climate change would favour the opening of gaps within the current vegetation zones, rather than a simple zonal shift of them. Dynamic and integrated conservation policies are required, that take account of the current and potential future spatial arrangement of species and their habitats, to assist species to respond to future environmental change.

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1. Introduction

The effect of climate change on the geographic distributions of species is often assessed in terms of potential climate envelopes (or spatial niches) shifting in latitude, longitude

or altitude (e.g. Thuiller, 2003; Segurado and Araújo, 2004; Thomas et al., 2004; Harrison et al., 2006). The IPCC report on the Regional Impacts of Climate Change (Watson et al., 1997) states that 'for mid-latitude regions, an average warming of 1–3.5 °C over the next 100 years would be equivalent to a

* Corresponding author. Tel.: +34 950 281045; fax: +34 950 277100.

E-mail address: gabriel@eeza.csic.es (G. del Barrio).

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poleward shift of the present geographic bands of similar temperatures (or isotherms) of approximately 150–550 km, or an altitudinal shift of about 150–550 m'. Such climate changes are likely to act as an important driving force on natural systems (Parmesan and Yohe, 2003; Thomas et al., 2004) and could threaten biodiversity and the conservation of species (Araújo et al., 2004).

Species–climate envelopes are derived using empirical–statistical models which combine the current distribution of species with environmental variables and then project their re-distribution under future climates (see review by Pearson and Dawson, 2003). Such approaches assume that the geographic distribution of species is constrained within minimum and maximum limits of a climate gradient and that the regional climate is fully realised as the main driver. These circumstances can occur in large and homogeneous landscapes where, for example, biotic interactions or the influence of soils or topography are negligible. They can also be detected when the surface of the Earth is examined at a coarse resolution. This is the main reason why climate change studies often adopt climate envelope approaches at broad (continental or global) scales (VEMAP members, 1995; Cramer et al., 2001; Thuiller et al., 2005; Harrison et al., 2006).

However, while continental or global species' distributions may be simulated using climate envelopes with reasonable success (Harrison et al., 2006), species can be found to exist outside the range limits predicted by this modelling approach (Loehle and LeBlanc, 1996). One reason for this is their actual populations being constrained or fragmented by more detailed environmental gradients that are detectable at finer resolutions. Topography is a good example: altitude or slope gradients can compensate for a lack of climatic suitability in terms of temperature or water availability. This is a microclimatic effect that might not be observed (or measured) at coarse spatial resolutions, which can be especially relevant at the spatial edge of a species' distribution. In addition to the effects of microclimate, other factors are also important in influencing the distribution of species at fine spatial resolutions. Many species display strong associations with land cover or specific habitat types (Thuiller et al., 2004) and the presence of species may depend on their tendency to disperse or migrate (Pearson and Dawson, 2003).

In locations where the influence of local microclimatic gradients dominate, because the scale length is shorter, the geographic distribution under consideration becomes patchier and the overall landscape fragmentation increases. Increases in fragmentation may have important effects on the autoecology of a species (Kappelle et al., 1999). The associated loss of connectivity will distort the meta-population arrangement within a region, with a likely increase in the number and respective isolation of population clusters. However, because connectivity takes place across the whole landscape matrix in most cases, the importance of land management and conservation policies becomes crucial as certain landscape categories (irrespective of whether these are anthropogenic, semi-natural, or natural) may become either corridors or barriers in the connection between those population clusters.

This paper describes an early attempt to integrate four models in a scale-dependent hierarchical framework to study the impacts of climate and land use change scenarios on

species' distributions at fine resolutions. The models include: SPECIES, a continental scale bioclimatic envelope model; downscaled SPECIES, a regional scale bioclimate and land use suitability model; a dispersal model; and ALCOR, a connectivity model. The integrated approach has been tested and applied to selected species in two case study regions with very different topographic and climatic conditions: East Anglia (southeast UK), with a gentle topography and in a largely homogeneous temperate climate; and Almeria (southeast Spain), with strong topographic contrasts and in a semi-arid Mediterranean climate. The implications for policy implied by our modelling study within the two regions are then discussed.

2. Methods

2.1. Case study regions

The East Anglia case study region in the UK encompasses the administrative districts of Norfolk, Suffolk and Cambridgeshire and has a total area of 12 592 km². The region has a relatively homogeneous low-lying topography with elevations ranging between 0 and 130 m above sea level. The climate is relatively dry and temperate with around 600 mm annual precipitation distributed fairly evenly throughout the seasons and mean temperatures ranging from around 4 °C in winter to 16 °C in summer. The main land uses in the region are arable cropping (cereals, sugar beet and potatoes) and intensive grassland. Several important species' habitats within the region are sensitive to agricultural land use patterns, two of which were selected for study: cereal field margins and lowland calcareous grassland. Four species within each habitat were modelled encompassing a range of taxa and dominant and threatened species. The species for cereal field margins were: *Silene gallica* (Small-flowered catchfly), *Papaver dubium* (Long-headed poppy), *Legousia hybrida* (Venus's looking glass) and *Lepus europaeus* (Brown hare). The species for lowland calcareous grassland were: *Helictotrichon pratense* (Meadow oat-grass), *Campanula glomerata* (Clustered bell-flower), *Hesperia comma* (Silver spotted skipper butterfly) and *Lysandra bellargus* (Adonis blue butterfly).

The Almeria case study region in Spain extends over 7087 km² in the southeast corner of the Iberian Peninsula. The area includes three major mountain ranges running in an east to west direction and several smaller elevations enclosing a tectonic basin that was opened to outer drainage in recent geological times and which is now heavily dissected into a large badlands area. As a result, the total relief exceeds 2000 m and the topography is generally rugged. The overall climate follows a Mediterranean pattern with two rainfall peaks in spring and autumn and a dry season during summer, but topographic variations mean it ranges from arid (the area includes the driest zone of the European Mediterranean) to humid. The area has been traditionally managed for arable cropping of cereals, almond and olive orchards, and grazing. However, progressive land abandonment since the second half of the 20th century has led to an extensive rangeland landscape acting as the hinterland to recent urban sprawl. The species selected for study were:

Quercus ilex (Holm oak) and *Q. faginea* (Portuguese oak), as representative of the natural zonal vegetation; *Pinus pinaster* (Maritime pine) and *P. halepensis* (Aleppo pine), as representative of largely favoured vegetation covers; and *Pistacia lentiscus* (Mastic) and *Chamaerops humilis* (European fan palm), as representative of dominant landscape covers in their respective habitats that are now threatened.

2.2. Data

Observed species' distributions were available gridded to a 10 km × 10 km resolution covering the UK from Preston et al. (2002) for plants, Asher et al. (2001) for butterflies, and Arnold (1993) for mammals. Distributions on a 1 km × 1 km grid covering the East Anglian case study area were obtained from Beckett et al. (1999) for Norfolk and County Records for Suffolk and Cambridgeshire. Species' distribution data on a 1 km grid for the Almeria case study region were extracted from the Spanish National Forest Map (Ruiz de la Torre, 2002). Climatic data containing 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) were modelled on a 1 km grid for Almeria using the equations of Sanchez Palomares et al. (1999) on the GTOPO30 Digital Elevation Model (EROS Data Center, 1996). The same variables were only available for the UK on a 5 km grid from the UK Climate Impacts Programme (Hulme et al., 2002). Values of potential evapotranspiration were computed from these climatic variables using the Penman formula (Penman, 1948). Land cover data on the percentage coverage of all land cover classes within each 1 km grid cell was derived from the 250 m resolution CORINE dataset in both case study regions.

Three climate change scenarios have been utilised for three time slices (2020, 2050 and 2080). They are based on two global climate models (HadCM3; Gordon et al., 2000; Pope et al., 2000 and PCM; Washington et al., 2000) and two SRES emissions scenarios (A2 and B1; Nakićenović et al., 2000) and are referred to as HadCM3 A2, HadCM3 B1 and PCM A2 throughout the paper. The scenarios were provided on a 10' latitude/longitude grid for Europe and are based on the ATEAM European climate scenarios (Mitchell et al., 2004), but use a different measure of inter-annual variability computed from the detrended 1981–1990 average. Further details regarding the creation of these scenarios are given in Harrison et al. (2006) and Rounsevell et al. (this volume). The European climate change scenarios at a 10' grid resolution were downscaled to a 1 km grid for the East Anglian and Almeria case study regions. A simple downscaling technique was used whereby the 10' climate change fields were directly applied to the higher resolution gridded baseline climatology. This method adds no new meteorological information and assumes that the spatial pattern of current (i.e. 1961–1990) climate remains the same into the future. Whilst more sophisticated methods are available, they are often expensive to implement and are based upon their own (often unquantifiable) assumptions. Alternatively, the method used was quick and easy to apply and enabled a range of scenarios to be explored which capture some of the uncertainty associated with different climate models and emissions scenarios.

The most severe changes in climate occur under the HadCM3 A2 scenario, where annual mean temperature averaged over the Almeria case study region increases by 4.1 °C by 2080 and by 3 °C over the East Anglian region. The HadCM3 B1 scenario shows a similar pattern of change, but the warming is slightly less severe. The PCM A2 scenario projects lower increases in annual temperature of 2.5 °C for Almeria and 1.9 °C for East Anglia by 2080. Changes in precipitation are also most severe under the HadCM3 A2 scenario, where they are projected to decrease in summer by 9.3 mm/month in Almeria and 20.7 mm/month in East Anglia by 2080. Winter precipitation is projected to increase under this scenario in East Anglia, by up to 16.9 mm/month, but decrease in Almeria, by up to 21.5 mm/month by 2080. Alternatively, the PCM A2 scenario shows much smaller decreases in precipitation for Almeria of approximately 6 mm/month in both summer and winter, and very small decreases in summer (0.8 mm/month average) and increases in winter (2.3 mm/month average) for East Anglia by 2080.

Land use change scenarios consistent with the same climate models, SRES scenarios and time slices have been utilised (Ewert et al., 2005; Rounsevell et al., 2005). These consist of changes in urban, cropland, grassland, bioenergy crops, forests and abandoned land classes simulated on a 10' latitude/longitude grid for Europe (EU25 plus Norway and Switzerland). The scenarios are based on a two-step modelling methodology: (i) the demand for each land use (defined as an area) is derived for each scenario at an aggregated spatial level, i.e. country or NUTS-2 (depending on the land use type); (ii) these land use areas are disaggregated (to a 10' grid) using spatial allocation rules and GIS data layers that include spatial planning zones. In addition, the methodology accounts explicitly for the competition between different land use types. This is implemented through a predefined hierarchy when allocating land uses in space that reflects both economic trends as well as the potential for spatial planning policy. Thus, for example, urban land use tends to take precedence over agriculture, which depending on the location characteristics usually dominates forestry. However, spatial planning policy at defined locations may limit urban development or protect certain types of land use and/or landscape structure, such as forests. The 10' land use changes were downscaled to a 1 km grid using a similar method and reasoning to that explained previously for the climate change scenarios. The 10' fields were directly applied to the higher resolution baseline CORINE land cover dataset. This involved randomly applying the projected land use changes between all relevant 1 km² baseline grid cells which fall within each 10' grid cell, but implemented according to the same land use allocation hierarchy as described above and within allocation constraints to ensure urban or arable land use could not be distributed at very high elevations.

2.3. Model description

Four models, which operate in a scale-dependent hierarchical framework, have been used for analysing the impacts of climate change on species' distributions within the two case study regions (Fig. 1). At the continental scale, climate is expected to be the dominant factor affecting the distribution

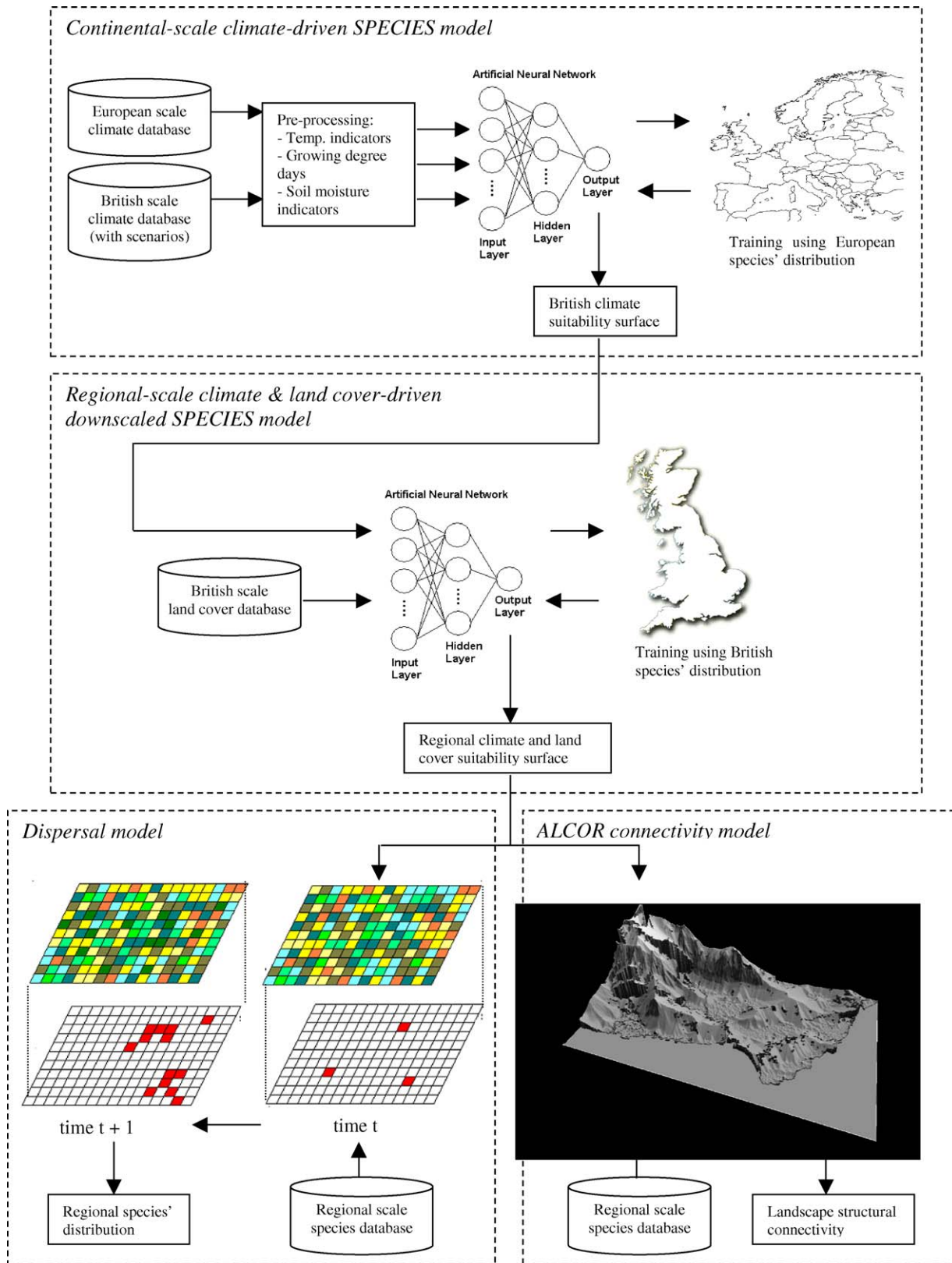


Fig. 1 – Schema showing modelling framework, illustrated for the UK case study region.

of species (Pearson and Dawson, 2003; Thuiller et al., 2004). The SPECIES model (spatial estimator of the climate impacts on the envelope of species) was used to characterise the current distribution of species at the European scale and to estimate their potential re-distribution under alternative climate change scenarios (Pearson et al., 2002). The SPECIES model employs an artificial neural network (ANN) to define bioclimate envelopes based on inputs generated through a climate-hydrological process model. The model is trained using existing empirical data on the European and North African distributions of species at a 0.5° latitude/longitude resolution (described in Harrison et al., 2006) to enable a wide climate space to be characterised that captures the climatic range of future scenarios. Once a network is trained and validated at the European scale, it is then applied at a finer spatial resolution within the case study regions. The SPECIES model and results from applying the model to 47 species at the European scale (including the species discussed in this paper) are reported in Harrison et al. (2006).

Although climate may be the principal factor influencing species' distributions at the broad-scale, other factors, such as habitat availability and dispersal ability, may be more important at regional scales. To study the combined effects of climate change and habitat fragmentation (as driven by changes in land cover) on species' distributions, the SPECIES model was downscaled (Pearson et al., 2004). Outputs from the continental scale climate-driven neural network are used as inputs to a second ANN, along with fine scale land cover data. This second ANN, trained on national or regional observed species' distributions at 1–10 km spatial resolutions, generates regional scale suitability surfaces for species. A suitability surface is defined as a landscape identifying areas where a species could potentially grow and reproduce, and is analogous to an approximation of the spatial manifestation of the fundamental niche (Pearson et al., 2004). This model provides an insight into the roles of climate and land cover as determinants of species' distributions and enables predictions of distributions under both climate and land use change scenarios to be examined.

The performance of the neural networks produced by the SPECIES and downscaled SPECIES models was statistically analysed using a randomly selected sub-sample of 30% of the distribution dataset which was extracted before model calibration. Sub-sampling a test dataset from the full dataset is a common approach, yet it is acknowledged that it can lead to over-optimistic estimates of predictive performance compared to validating against more independent test data (Araújo et al., 2005a). We assessed predictive performance using the area under the receiver operating characteristic curve (AUC)—AUC is a measure of prediction accuracy derived 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. Three decision

thresholds based on the ROC curve have been applied which maximise the agreement between observed and simulated distributions and capture 90 and 95% of observed presences. Further details concerning the model validation and definition of decision thresholds are provided in Pearson et al. (2004).

The ability of species to track changes in the regional suitability surfaces simulated by the downscaled SPECIES model will be dependent on the dispersal mechanisms by which migrations occur, and the underlying landscape connectivity for such a migration to effectively occur. Thus, the 1 km² simulated suitability surfaces for each region were coupled with a dispersal model and a connectivity model. These two models are complementary in their respective approaches: the dispersal model is dynamic and process oriented, therefore it has an in-built mechanism to simulate the time dimension; however, the connectivity model is static and focused on landscape structure, time not being explicitly incorporated.

The dispersal model is based on a spatially explicit cellular automaton which simulates the stochastic dispersal of species in terms of two main processes: the release of a number of propagules by an existing population and the redistribution of the propagules according to a dispersal function (Pearson and Dawson, 2005). The model operates through three basic steps: (i) survival; (ii) within-cell population dynamics; (iii) dispersal. Cell suitability is defined as binary suitable or unsuitable, and the suitability changes across time steps according to the regional suitability surfaces produced by the downscaled SPECIES model for the climate and land use change scenarios. Long distance dispersal is incorporated within the model enabling investigation of the potential for species to migrate rapidly under future climate change. The model required parameterisation for six species-dependent variables before it could be applied within the case study regions. These are maximum and mean dispersal distance, the shape parameter for the dispersal kernel, net reproductive rate, years to reach reproductive maturity and fecundity. Information on each variable was gathered from an extensive search of the ecological literature, supplemented by expert opinion. As specific information was rarely available, categories were defined to assist with the parameterisation of the model based on sensitivity analyses showing the implications of independent and combined variations in the main parameters. These categories were:

Shape of the dispersal kernel (c)

- Fat-tailed distribution (0.5)—birds, insects and herbaceous with light, wind-dispersed seeds
- Exponential distribution (1.0)—trees, very heavy seeds
- Gaussian distribution (2.0)—mammals

Net reproductive rate (R)

- Slow growth (1.5)—perennials, trees and less than univoltine organisms
- Medium growth (2.0)—annuals, univoltine organisms
- Rapid growth (3.0)—multi-voltine plants and organisms

Fecundity. Five categories, ranging from low (parameter value = 1) for species that produce few seeds, to high (value = 5) for species that produce many seeds.

Since dispersal is simulated as a stochastic (non-deterministic) process, the model is run using a Monte Carlo approach. Thus, the dispersal process was run 5000 times so as to build up a probability surface identifying those cells that are more/less likely to be populated under certain dispersal assumptions.

The ALCOR connectivity model (del Barrio et al., 2000) addresses the ability of a certain species population to transit across a landscape, given the environmental niche of the species, the spatial arrangement of its populations, and the spatial heterogeneity of the territory. Connectivity is taken in ALCOR as a spatial property because it is concerned with relative differences between locations, not with the absolute affinity of the species for individual sites, hence it can detect functional links between locations that are not contiguous in the landscape (O'Neill et al., 1988; Gardner et al., 1993). It is also considered as a landscape attribute, but it is extrinsic because it must be parameterised for different taxa or functional groups. Finally, connectivity is assumed to be a structural and static property because it is not changed by the intensity of transits. Moreover, the time dimension is purposely excluded and the results from the model should be interpreted as a relative assessment of possible transit paths, not as the probability that a concrete population will disperse through such paths.

ALCOR runs within the frame of a raster Geographic Information System. Input data are: the geographic distribution of the species (normally available through surveys and regional databases), its environmental suitability (in the current implementation it accepts directly suitability surfaces generated by the downscaled SPECIES model), and its dispersal scale (a single variable that is parameterised as the threshold distance that identifies two non-contiguous distribution patches as different populations). The landscape friction is coded from the suitability surface. Then, the spatial configuration of populations is used to compute a cost surface that reflects the cumulative cost of reaching each map location from the nearest population. The cost surface is used in two forms to assess the landscape connectivity for that species. First, its mean value is interpreted as a lumped, non-spatial estimator of the overall transit difficulty. Second, its roughness is used as an overall estimator of connectivity through the assumption that, the more complex the cost surface, the more deterministic will be its effect on the population transit. The fractal dimension is used as a measure for this purpose because it results in a single number in the range 2–3 (for a surface) making interpretation easier, and because it takes explicit account of spatial scale if computed through the semi-variogram method (Xu et al., 1993). The cost surface is spatially explicit, therefore a third use is to assess likely transit paths between populations, as well as to identify natural neighbourhood relationships among them.

In ALCOR, the whole procedure is performed once using all the populations, and the resulting fractal dimension is used for comparing different suitability surfaces associated with the different scenarios. Then, cost surfaces are computed by suppressing one population at a time to assess the relative contribution of the eliminated population to the overall connectivity for a given scenario. This assessment is made in terms of the spatial scale at which the extinction of the

concerned population creates a disturbance at the landscape level in the study area.

3. Results

3.1. East Anglia case study region

The European-trained SPECIES models show excellent discrimination ability with AUC values ranging from 0.94 to 0.99 for the eight species selected for the East Anglian region (Harrison et al., 2006; see Table 3). These models based on bioclimatic variables were applied at a 5 km × 5 km spatial resolution at the national scale for Britain. Results for the four species associated with lowland calcareous grassland show progressive northwards increases in climate space for the two butterfly species (*H. comma* and *L. bellargus*) and a mixture of gains and losses for the plant species (*C. glomerata* and *H. pratense*) (see Table 1). For *C. glomerata*, climate space is lost from Scotland, but gained in Wales and parts of western England. The distribution of *H. pratense* gradually spreads westwards over time under all the scenarios, but by 2080 the distribution becomes quite fragmented with large losses in southern England under the PCM A2 scenario and in eastern England and Scotland under the HadCM3 A2 scenario. Results for the four species associated with cereal field margins show general increases in climate space for *S. gallica* and *P. dubium*, but a mixed response for *L. hybrida* and *L. europaeus*. Losses are particularly severe for *L. europaeus*, where 65% of its climate space disappears from southern and eastern England and eastern Scotland by 2080 under the HadCM3 A2 scenario. Alternatively, the PCM A2 scenario causes much less drastic losses of only 8% in eastern England by 2080 (Fig. 2).

Data on observed species' distributions were available for all eight species at a 10 km × 10 km spatial resolution. These were used to train downscaled SPECIES models on bioclimatic and land cover variables at the national scale. The inclusion of land cover data improved the ability of the models to capture the observed distribution for all species (Table 2). Pearson et al. (2004) and Araújo et al. (2005b) also found that the incorporation of land cover data significantly improved purely climate-driven predictions for between 26 and 50% of the species studied when downscaling distributions to fine resolutions. Alternatively, Thuiller et al. (2004) showed that the addition of land cover variables to pure bioclimatic models at coarse resolutions for Europe did not always improve predictive accuracy. This supports the proposition of Pearson et al. (2004) that environmental correlates with species' distributions must be addressed at an appropriate spatial scale. The improved model ability found here is illustrated for *L. hybrida* in Fig. 3, where predictions based on bioclimate alone show a much more widespread suitability than is seen in the observed distribution. However, the climate and land cover model removes the climate space from Scotland and northern England, resulting in a much closer simulated distribution to the observed. Models for *L. europaeus* and *H. pratense* resulted in poor statistics both with and without land cover due to highly fragmented observed distributions (Table 2). Visual comparison of the bioclimate and land cover models for *H. comma* and *L. bellargus* showed that they were unable to

Table 1 – Gains (+) and losses (–) in regional climate space (%) under two scenarios

Species	HadCM3 A2 scenario			PCM A2 scenario		
	2020	2050	2080	2020	2050	2080
UK						
<i>Hesperia comma</i> ^a	+404/0	+589/0	+752/0	+301/0	+447/0	+681/0
<i>Lysandra bellargus</i> ^a	+182/0	+243/0	+347/0	+152/0	+206/0	+287/0
<i>Campanula glomerata</i>	+15/–11	+22/–14	+27/–24	+7/–12	+14/–12	+22/–16
<i>Helictotrichon pratense</i>	+19/–7	+20/–14	+19/–32	+16/–6	+17/–14	+16/–41
<i>Silene gallica</i>	+25/0	+32/0	+46/0	+22/0	+31/0	+41/0
<i>Papaver dubium</i>	+4/0	+5/–2	+5/–7	+4/0	+5/–2	+5/–9
<i>Legousia hybrida</i>	+9/–14	+9/–19	+9/–20	+8/–10	+9/–15	+12/–14
<i>Lepus europaeus</i> ^b	+15/–15	+15/–32	+12/–65	+17/–8	+18/–8	+23/–7
Almeria, Spain						
<i>Pistacia lentiscus</i>	+32/0	+50/0	+58/–29	+27/0	+39/0	+52/0
<i>Chamaerops humilis</i>	+4/0	+7/0	+7/0	+2/0	+5/0	+7/0
<i>Pinus halepensis</i>	+1/0	+1/0	+1/–7	+1/–5	+1/–6	+1/–8
<i>Pinus pinaster</i>	0/–53	0/–72	0/–86	0/–42	0/–55	0/–71
<i>Quercus ilex</i>	0/0	0/0	0/–31	0/0	0/0	0/0
<i>Quercus faginea</i>	0/0	0/0	0/–13	0/–4	0/–1	0/0
^a Insect.						
^b Mammal.						

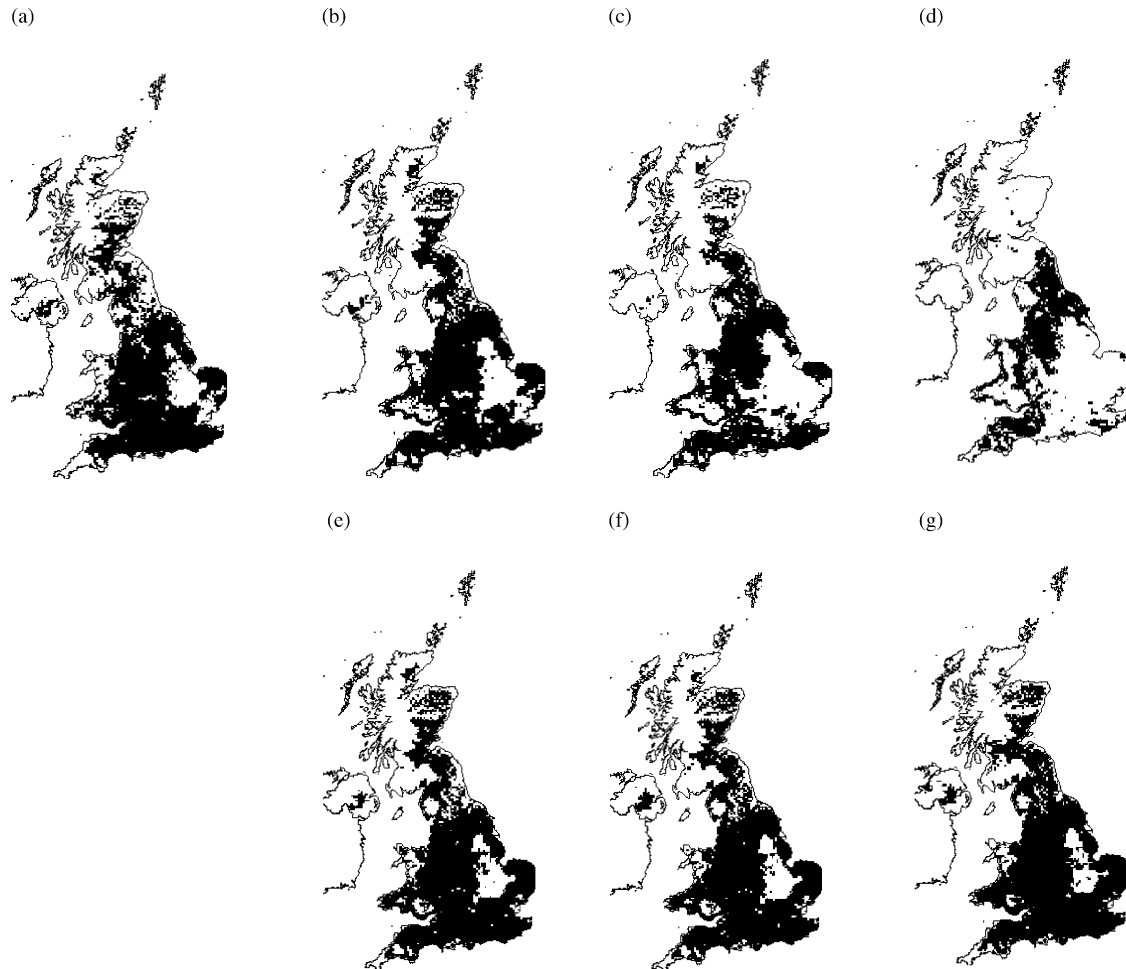


Fig. 2 – Potential climate space for *Lepus europaeus* in Britain for (a) baseline (1961–1990); (b) HadCM3 A2 scenario for 2020; (c) HadCM3 A2 scenario for 2050; (d) HadCM3 A2 scenario for 2080; (e) PCM A2 scenario for 2020; (f) PCM A2 scenario for 2050; (g) PCM A2 scenario for 2080.

Table 2 – Independent testing of the downscaled SPECIES model based on bioclimate variables only and bioclimate and land cover variables against national scale observed species' distributions using the area under the receiver operating characteristic curve (AUC)

Species	AUC	
	Bioclimate	Bioclimate and land cover
Lowland calcareous grassland		
<i>Hesperia comma</i> ^a	0.88	0.91
<i>Lysandra bellargus</i> ^a	0.88	0.90
<i>Campanula glomerata</i>	0.71	0.83
<i>Helictotrichon pratense</i>	0.62	0.69
Cereal field margins		
<i>Silene gallica</i>	0.75	0.79
<i>Papaver dubium</i>	0.84	0.85
<i>Legousia hybrida</i>	0.86	0.90
<i>Lepus europaeus</i> ^b	0.56	0.62

^a Insect.
^b Mammal.

replicate the observed distributions better than the models based on bioclimate alone, despite having reasonable statistics, due to the current rarity of these species in Britain (Table 2).

The climate change scenarios were applied to the four downscaled SPECIES models which showed at least reasonable validation statistics (AUC > 0.7; Table 2) and an improvement in the simulation from the original SPECIES model. Similar patterns of response to those already described for the bioclimate-only models were predicted, but the simulated distributions were more fragmented due to the influence of current land use patterns. Independent and combined climate and land use change scenarios were applied to the models at a 1 km² resolution within the East Anglian case study region. These resulted in further frag-

mentation of species' distributions as the land use change scenarios suggest fairly large reductions in arable land use classes, which are particularly relevant for the cereal field margin species. This is illustrated in Fig. 4 for *S. gallica*. When the climate change scenarios are applied on their own, suitability increases in the north of the region (Norfolk), but decreases in the west of the region (Cambridgeshire). Alternatively, when the land use change scenarios are applied on their own, suitability decreases virtually everywhere reflecting the decreases in arable land use. Finally, when the climate and land use changes are applied in combination, there is a slight improvement in suitability in the northeast of the region compared to the baseline, but a worsening throughout much of the rest of East Anglia.

The 1 km suitability surfaces from the combined climate and land use change scenarios for East Anglia were linked with the dispersal model to estimate the likely ability of species to track the predicted changes in their distributions and results are summarised in Table 3. *S. gallica* and *P. dubium* are not expected to disperse very far as they have low mean and maximum dispersal distances (0.001 km and 1 km, respectively) and their underlying suitability surfaces are highly fragmented, particularly under the A2 SRES scenarios where considerable arable land is lost. This results in several grid cells containing observed presences no longer falling within suitable climate and land use space, reducing the potential size of the future distribution and the opportunities for dispersal. On the other hand, *L. hybrida* and *C. glomerata* are more successful in dispersing further as their underlying suitability surfaces are more continuous under the scenarios and they have a greater maximum dispersal distance (10 km).

The same 1 km suitability surfaces, along with the respective observed distributions, were input to the ALCOR model to assess the connectivity of baseline and scenario landscapes. Fig. 5 shows the attributes of the resulting cost surfaces, both in terms of their overall mean and their fractal

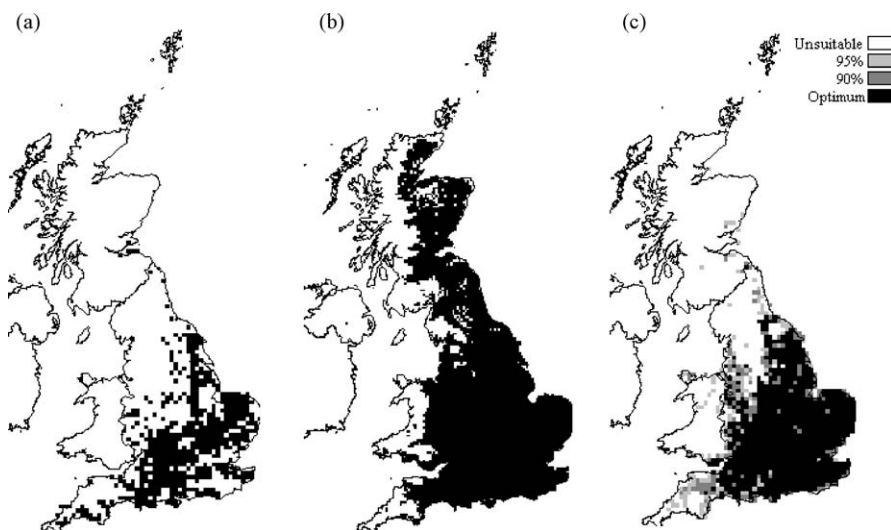


Fig. 3 – Results from the downscaled SPECIES model for *Legousia hybrida* in Britain: (a) observed distribution; (b) simulated baseline (1961–1990) distribution based on bioclimate only; (c) simulated baseline (1961–1990) distribution based on bioclimate and land cover variables. The areas in black in (c) are based on maximising the agreement between observed and simulated distributions ('optimum' in the key), whilst areas in dark and light grey capture 90 and 95% of the observed presences, respectively.

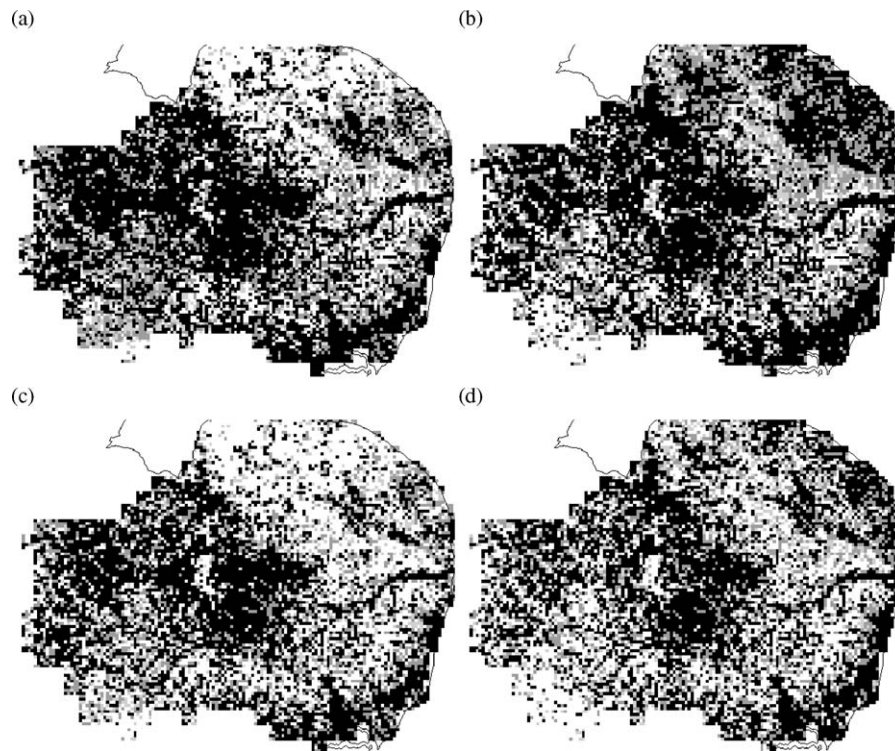


Fig. 4 – Independent and combined application of the climate change and land use change scenarios for *Silene gallica* in East Anglia: (a) Baseline (1961–1990) suitability; (b) suitability under the HadCM3 A2 climate change scenario for 2080; (c) suitability under the HadCM3 A2 land use change scenario for 2080; (d) suitability under the combined HadCM3 A2 climate and land use change scenarios for 2080. The areas in black are based on maximising the agreement between observed and simulated distributions, whilst areas in dark and light grey capture 90 and 95% of the observed presences, respectively.

dimension or geometric complexity. Of the four species tested, only *L. hybrida* shows a consistent decrease in the overall transit cost coupled with an increase in the fractal dimension over time. Because the fractal dimension reflects the spatial variance, the decrease in the mean transit cost must be interpreted in this case as being due to the creation of local depressions in the cost surface rather than to a generalised lowering of it. This results in an increased fragmentation that therefore facilitates transits. The trends shown by *H. pratense* and *P. dubium* are different, as both the mean and the fractal dimension of the cost surfaces increase over time under most of the scenarios, suggesting a progressive deterioration of ecological connectivity. Finally, *S. gallica* shows no sharp changes in the overall cost, but a general decrease in its fractal dimension, which is interpreted as a homogenization of its transit space.

3.2. Almeria case study region

The European-trained SPECIES models show excellent discrimination ability with AUC values ranging from 0.93 to 0.99 for the six species selected for the Almeria region (Harrison et al., 2006; see Table 3). Results from applying these models, trained on bioclimatic variables, to the 1 km² resolution datasets for Almeria show general increases in climatic suitability over time for two species (*C. humilis* and *P. lentiscus*) (see Table 1). The areas of high elevation which are classified as unsuitable in the baseline simulations gradually become suitable. However, this is balanced by losses in suitability in the south of the region by 2080 for *P. lentiscus*, but only under the HadCM3 A2 scenario. *P. halepensis* shows a small increase in suitability in the mountainous parts of Almeria, but loses climate space in the south in all time slices for the PCM A2

Table 3 – Gains (+) and losses (–) in species' distributions (number of grid cells) based on bioclimate, land cover and dispersal ability under two scenarios

Species	Base presences	HadCM3 A2 scenario			PCM A2 scenario		
		2020	2050	2080	2020	2050	2080
<i>S. gallica</i>	68	+153/–13	+152/–16	+197/–13	+151/–14	+146/–18	+190/–14
<i>P. dubium</i>	644	+1166/–43	+1184/–41	+1466/–35	+1167/–43	+1184/–41	+1476/–35
<i>L. hybrida</i>	783	+1845/–7	+1912/–7	+2486/–7	+1845/–7	+1913/–7	+2488/–7
<i>C. glomerata</i>	58	+1007/–1	+2263/–1	+3531/–2	+1004/–1	+2264/–1	+3530/–2

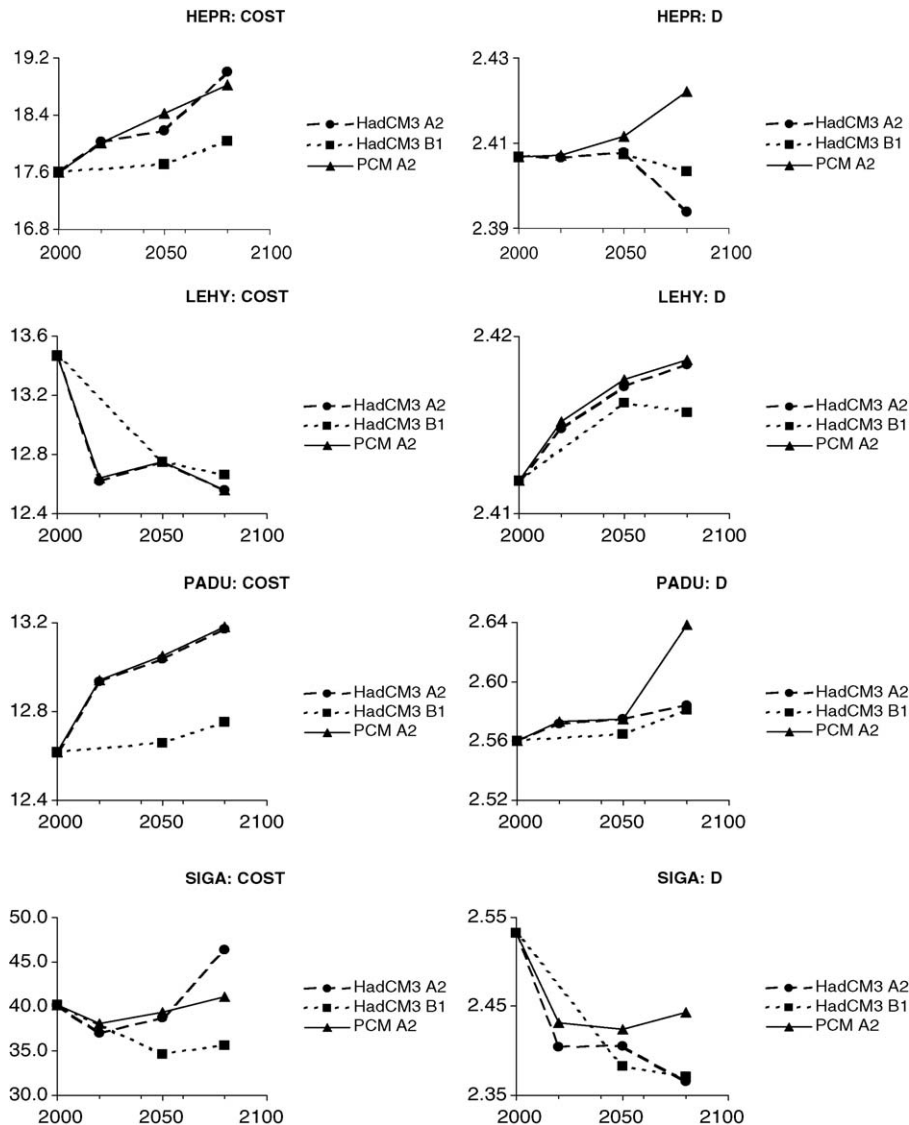


Fig. 5 – Results of the ALCOR connectivity model for the East Anglia species: overall mean (COST) and fractal dimension (D) of the cost surfaces for the three climate scenarios. Abbreviations: HEPR: *H. pratense*; LEHY: *L. hybrida*; PADU: *P. dubium*; SIGA: *S. gallica*.

scenario and just by 2080 under HadCM3 A2. The other three species (*P. pinaster*, *Q. ilex* and *Q. faginea*) show no gain in climate space and a general decrease in climatic suitability throughout the region for *P. pinaster* under all the scenarios, but only in the south and east of Almeria for *Q. ilex* under the HadCM3 A2 and B1 scenarios for 2080. The current observations for *Q. ilex* all remain within areas of suitable climate up to 2080, but those for *P. pinaster* are classified as climatically unsuitable by 2050 under both HadCM3 scenarios and by 2080 under the PCM scenario (Fig. 6). Results for *Q. faginea* show little change in suitability for the 2020 and 2050 time slices of both HadCM3 scenarios followed by a large decrease in climate space in 2080. Alternatively, the PCM A2 scenario produces a small loss of climate suitability in the south and east of Almeria in 2020, which is then gradually ameliorated in the 2050 and 2080 time periods.

Observed species' distributions were only available at a 1 km² resolution for three species (*Q. ilex*, *P. pinaster* and *P.*

halepensis) and these were used to train the downscaled SPECIES models, which incorporated land cover data. However, the species chosen are very rare within the region and observations covered less than 3% of the grid squares. This was insufficient to build a reliable relationship within the downscaled SPECIES model. Hence, the 1 km² suitability surfaces based on bioclimate alone were linked with the species' dispersal model to simulate the extent to which gains and losses in climate space are likely to be realised. *Q. ilex* was predicted to increase its distribution from covering 2.5% of the region currently to 16% in 2020, 19% in 2050 and 26% in 2080 under all the scenarios (Fig. 7). *P. halepensis* was also simulated as increasing its distribution from 0.4% of the region in the baseline to 3.2% in 2020, 5.8% in 2050 and 7.8% in 2080. Alternatively, *P. pinaster* only occurs in two 1 km grid squares in the current observations and these are lost by 2050 under the HadCM3 A2 and B1 scenarios and by 2080 under the PCM scenarios. However, there is some opportunity for the species

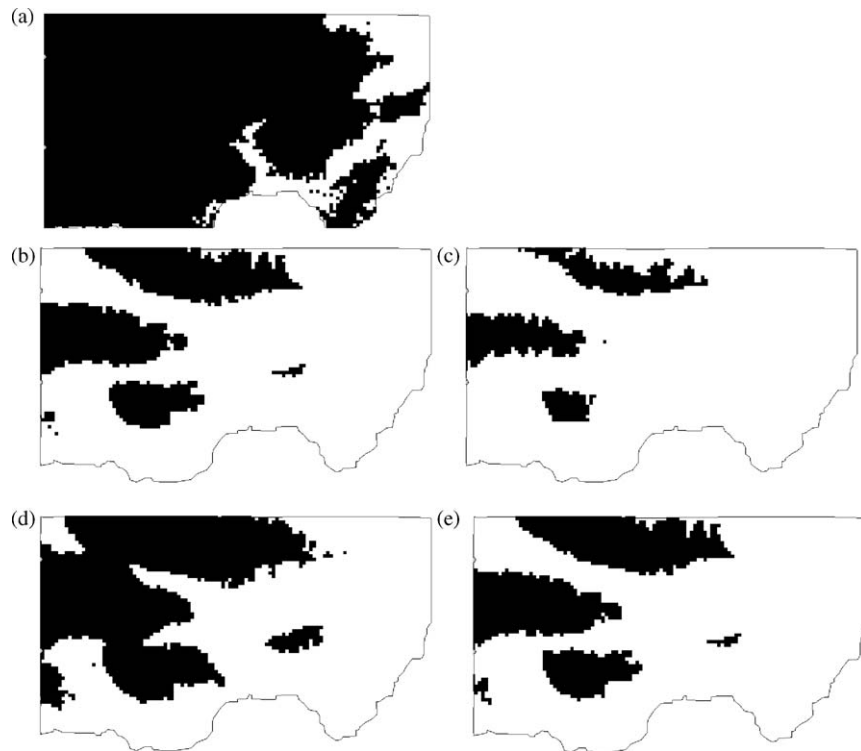


Fig. 6 – Potential climate space for *Pinus pinaster* in Almeria for (a) baseline (1961–1990); (b) HadCM3 A2 scenario for 2050; (c) HadCM3 A2 scenario for 2080; (d) PCM A2 scenario for 2050; and (e) PCM A2 scenario for 2080. The two observed presences are shown in grey along the western border of the region.

to disperse in the time available to neighbouring grid cells, which are climatically suitable.

Though *Q. ilex* has the potential to increase its distribution according to the dispersal model, the climate surfaces simulated for 2080 at the locations of the observed presences show an average decrease in suitability of 1.3% for the HadCM3 A2 scenario, 0.8% for HadCM3 B1, and 0.4% for PCM A2. While such values do not seem large, the three series of scenarios cause a significant, albeit non-homogeneous impact on the landscape connectivity for this species (Fig. 8). The HadCM3 A2 scenario shows the largest effect, with the mean transit cost doubling by 2080. The fractal dimension of the associated cost surfaces also increases progressively with time, which is interpreted as an increment of the spatial contrast between suitable and non-suitable areas. Because of the overall decrease in climate suitability, this means in turn that, the lower the initial suitability, the faster its deterioration with time under this scenario. The HadCM3 B1 scenario follows the same pattern, but somewhat attenuated. The PCM A2 scenario shows a different trend: the transit cost increases at a much slower rate, and the fractal dimension shows a slight decrease by 2080. This predicts a smaller but more homogeneous (in spatial terms) impact on connectivity.

The other tree species follow a relatively similar pattern of increased transit costs over time, but with their own specific results concerning spatial heterogeneity. *Q. faginea* is almost identical in terms of overall cost evolution, but the sharp increase of fractal dimension under PCM A2 by 2020 suggests an improved connectivity because of local depressions in the cost surface. However, the high cost with a relatively low

fractal dimension by 2080 under HadCM3 A2 suggests a homogeneously unsuitable environment. *P. pinaster* exhibits very fast increases in cost over time for all scenarios except for HadCM3 A2 by 2080, under which only a few disconnected patches remain moderately suitable and most of the territory becomes a barrier. In such circumstances, the associated high fractal dimension can be interpreted as a likely extinction of this species.

C. humilis shows a decrease both in cost and in fractal dimension under all scenarios, which indicates improved connectivity associated with the progressive warming and aridification, which in turn is consistent with the thermophilous character of this species. *P. lentiscus* also shows a general cost decrease, but the relatively high associated fractal dimensions during the intermediate time slices, when cost is at a minimum, suggests that the improvement in connectivity is reached gradually through the creation of suitable areas that grow over time.

4. Discussion and conclusions

4.1. Model limitations and uncertainties

Four models have been integrated to predict the potential impacts of climate and land use change on species' distributions at the regional scale. The approach is based on a scale-dependent hierarchical framework which explicitly links broad-scale climatic drivers of species' distributions with regional scale land use drivers and fine-scale processes

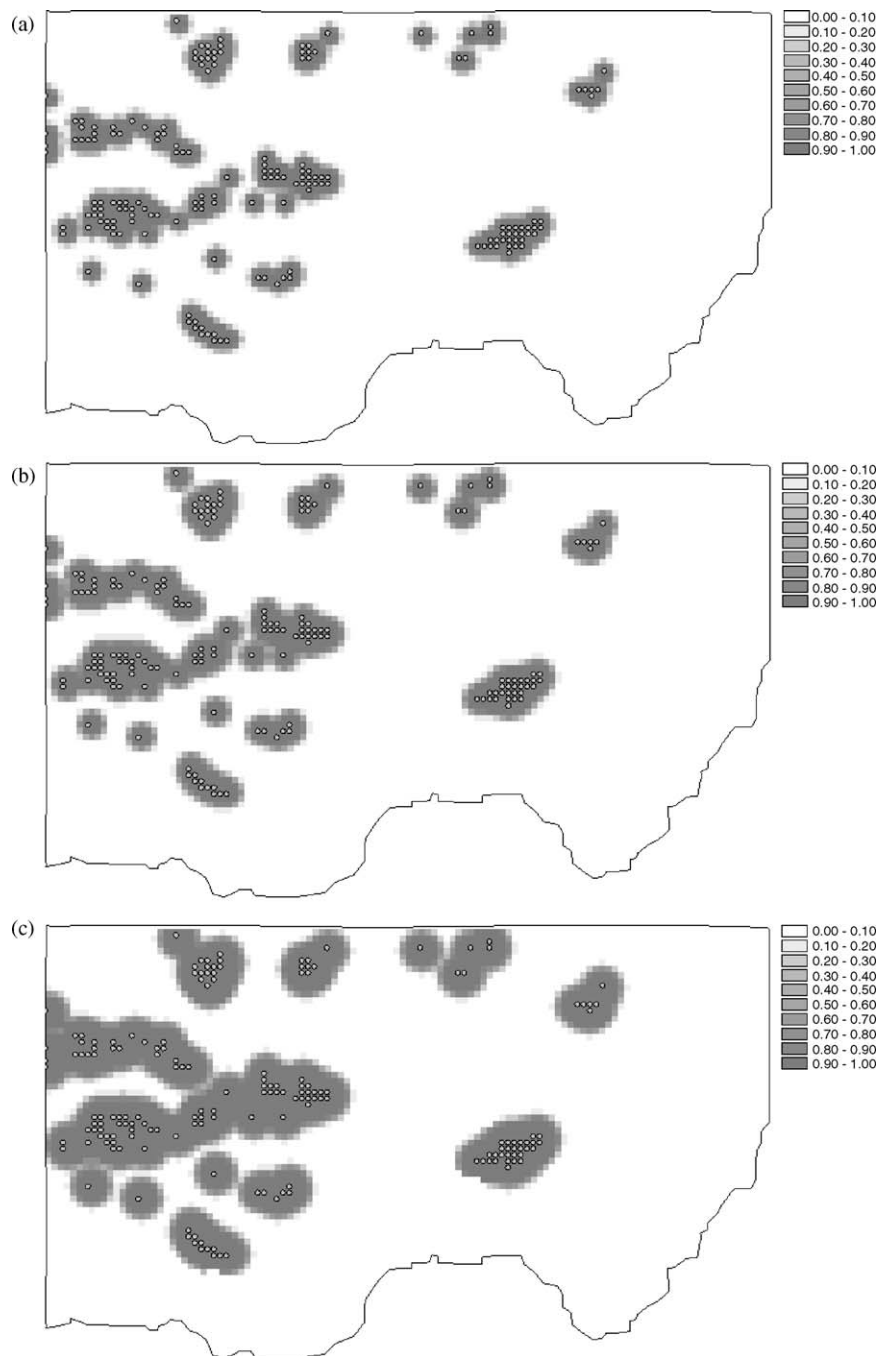


Fig. 7 – Probability of dispersal from observed populations for *Quercus ilex* in Almeria under all climate change scenarios: (a) 2020; (b) 2050; (c) 2080.

including species' dispersal and local landscape connectivity. The integrated modelling approach has been applied in two contrasting regions under three climate change scenarios. The scenarios capture some of the range of uncertainty associated with climate models and future emissions of greenhouse gases, but this represents only a limited sample of all available scenarios (IPCC, 2001). Thus, model predictions should be interpreted with due caution and should not be seen as encompassing the full range of possible outcomes. The models only examine the impacts of averaged climatic changes. The increased frequency and magnitude of extreme events, such

as droughts or storms, may have significant impacts on species' distributions that are not taken into account.

There are also important limitations to the predictive capacity of the simulation models used in this paper. Limitations of the SPECIES model are discussed in detail in Harrison et al. (2006), including the benefits and limitations of neural networks compared to other modelling techniques, autonomous adaptive changes to species in response to climate change, and the importance of biotic interactions between species, such as competition, predation and symbiosis with other species.

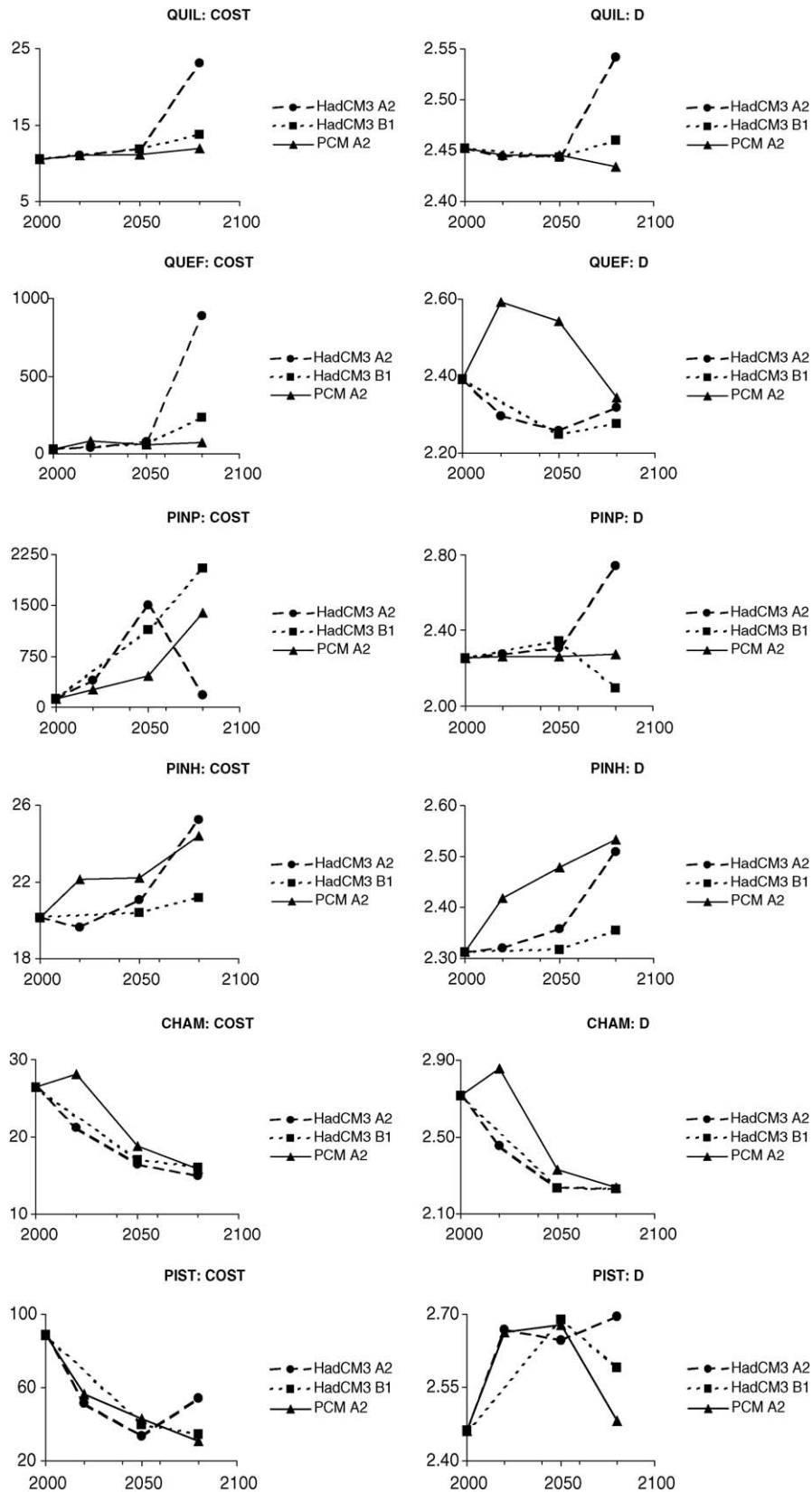


Fig. 8 – Results of the ALCOR connectivity model for the Almeria species: overall mean (COST) and fractal dimension (D) of the cost surfaces for the three climate scenarios. Abbreviations: QUIL: *Q. ilex*; QUEF: *Q. faginea*; PINP: *P. pinaster*; PINH: *P. halepensis*; CHAM: *C. humilis*; PIST: *P. lentiscus*.

The SPECIES and downscaled SPECIES models were originally developed for plants and birds, and the application to mammals adds an extra degree of uncertainty. However, similar models have been successfully applied to mammals in other parts of the world (e.g. Anderson et al., 2002). The dispersal model is also best suited to wind-dispersed plants because mammals are much more complicated since they make decisions about where to go (e.g. following rivers or looking for a mate). Hence, the random direction assumption in the dispersal model is not appropriate for mammals and the model was not applied to *L. europaeus* in this study.

The different abilities of species to migrate and thereby track changes in the predicted suitability surfaces is a function of the parameterisation of the dispersal model. However, there is scant data on the dispersal capabilities of most species and, thus, some of the dispersal parameters had to be derived from knowledge of other species or based on expert opinion. The sensitivity of dispersal modelling to the input parameter values has only undergone limited testing and future work could include the use of various parameterisations for each species, so that different ‘scenarios’ of potential migration ability can be derived.

To thrive in a landscape is not the same as to transit across it. In this work, suitability surfaces from the downscaled SPECIES model have been used as an input to the ALCOR model to parameterise transit frictions. This can result in an underestimation in connectivity, as most species can endure harsher conditions during transits than when reproducing within settled populations. However, the relatively coarse resolution used in the model minimises this problem as both transit and reproduction conditions can be expected to be comparable within 1 km cells at the edge of a species’ distribution. Therefore, only purely transit cells are likely to have been excluded from the results.

The modelling framework has been designed to take best advantage of the available data at different spatial resolutions. However, the availability and accuracy of data on observed species’ distributions for Europe and the case study regions varies considerably between species and locations. In particular, the assumption that observed species absences are true absences and not a result of insufficient sampling is a known problem with data accuracy (Griffiths et al., 1999; Araújo et al., 2005b). Shortfalls in the availability of habitat data also led to the assumption in the downscaled SPECIES model that land cover is a suitable surrogate for habitat availability. Base errors arising from data limitations are therefore unavoidable and their effects on model performance needs further exploration. However, the level of success that has been achieved in modelling species’ distributions has demonstrated that biogeographical trends can be identified regardless of the imperfect data that is so often all that is available in ecological studies (Pearson et al., 2004).

4.2. Comparison of a temperate and a Mediterranean area

The gentle lowlands of East Anglia create relatively short topographic gradients that need to be studied at a higher resolution than used in this work. As a result, the changes predicted by the three climate scenarios can be expected to

shift suitability over the geographic region, with a low impact on the spatial texture of suitability itself. The northwards displacement of suitability for *S. gallica* under the climate change scenarios is a good example of this trend.

On the other hand, land use change is the main factor driving alterations in the spatial properties of suitability in East Anglia. The land use change scenarios have an impact on suitability that is detected at scale lengths shorter than those resulting from climate change, as is suggested for *S. gallica* by the generalised (i.e. no apparent geographic pattern) worsening of suitability. However, such a generalised impact created by independently changing land use can have an extensive effect on the combined climate and land use suitability by fragmenting the climatic pattern. This is illustrated by two contrasting results of the connectivity analysis. *P. dubium* shows a raised mean transit cost under all three scenarios, and the increased fractal dimension suggests that it is due to additional roughness of the cost surfaces caused by fragmentation of suitable land uses. Hence this species suffers a general worsening of connectivity, which is also reflected by the results of the dispersal model. On the other hand, *L. hybrida* shows a consistent decrease in mean costs under the same scenarios, again with an increased roughness of the cost surfaces. This can only be interpreted as being due to local depressions appearing in the cost surfaces through time, which would be caused by land use fragmentation. In this case, the outcome is an improvement of connectivity. This latter case supports the idea that fragmentation and connectivity should not be interpreted in a uni-directional manner (i.e. fragmentation being ‘bad’ and connectivity being ‘good’), as scattered patches of improved suitability within a homogeneously unsuitable environment will create a fragmentation that actually facilitates connectivity.

The case study region of Almeria is very different to East Anglia, because strong topographic gradients create a variety of climate zones. The shift of these zones as a result of climate change does not only occur horizontally, but also vertically along altitudinal gradients. The resulting pattern of suitability will depend on whether the change favours the natural preferences of a species. But in general terms, an upwards shift of suitability will mean a fragmentation, while a downwards shift will mean a coalescence of potential space (Neilson, 1993).

This is supported by the results. *C. humilis* is a palm tree of thermophilous affinities, its current distribution in the area is a relict from the tertiary period, and it is limited to the lowest altitudes close to the seashore. The predicted warming associated with all the climate change scenarios increases not only its bulk area of potential distribution, but the transit cost also becomes lower and more homogeneous spatially. If only regional climatic factors were considered, this species could be expected to extend its potential space under the tested conditions.

Next in altitude is *P. lentiscus*, a shrub that is typical of Mediterranean garriga and macchia. Its present-day distribution within the study area consists of two main populations close to the sea, and located at opposite corners of the study area (southwest and northeast). As for *C. humilis*, suitability improves over time due to the progressive warming,

but in this case the pattern is slightly different because it involves mountainous areas: high divides are no longer a barrier, and mid and footslopes become likely transit spaces. As a result, the overall mean transit cost decreases, and the corresponding surfaces become more complex or fragmented. This pattern is similar to that shown by *L. hybrida* in East Anglia, and here too connectivity is favoured by an increased fragmentation.

Trends for montane species in the Almeria case study are well represented by *Q. ilex*, which because of the present-day aridity is confined to the upper belts of mountains. The area of potential distribution contracts under all the climate scenarios, but as mountains are widespread in the area, no significant loss of the species is detected in the region. However, the core areas of suitability are centred more and more on top of the mountains, and for that reason the average transit cost across the whole territory increases accordingly, as well as the fractal dimension of the cost surface. This is particularly noticeable beyond 2050 for all the scenarios. Hence, the impact of climate change for this and other montane species in Almeria is probably stronger in terms of loss of connectivity than in terms of loss of potential space.

4.3. Implications for policy

This paper has shown how species in the case study regions vary in their ability to respond through dispersal to the modelled changes in their suitable environmental space, based on both climate and land use change, with many being unable to fulfil their potential range, thus furthering their vulnerability. In the case of *P. dubium* the difficulties in fulfilling its ranges stem partly from the fragmentation of the habitat hindering dispersal. This is repeated for other species, such as *H. pratense* where the transit costs increase as the result of a decrease in connectivity. These increases in costs are even more important when combined with loss of suitable climate space, as in the case of the tree species in Almeria, e.g. *Q. ilex*.

A consideration of the implications for policy, therefore, should be extended to include those policies that impact on the changing transit costs and which hinder the autonomous adaptation of species (Berry et al., 2006). Agriculture will have a very significant role in influencing the ecological connectivity of the landscape for species dispersal, and thus transit costs, as it is the predominant land use in Europe. For the East Anglian species examined in this paper, which are associated with agro-ecosystems, the continuation of such systems is important in helping them adapt to climate change. Conservation policy therefore, needs to be combined with agricultural policy, so that the transit costs for species can be minimised through maintaining habitats and thus landscape connectivity. Already in the UK there are a number of schemes, such as Environmental Stewardship and Wildlife Enhancement, which seek to improve biodiversity in agro-ecosystems. These need to be combined with measures such as Habitat Action Plans (in the UK), to ensure the continuation of habitats of appropriate quality. As has been shown by this paper, both their current and especially their future spatial arrangement also should be taken into account when

formulating and implementing policies, as species and their habitats will be moving in response to climate change and thus a more dynamic approach is necessary.

In the case of Almeria, climate change poses a particular problem for the montane species, as suitable sites become confined to mountaintops and thus are more fragmented and here the conservation policy options are more limited. For the more lowland species such as, *C. humilis* and *P. lentiscus*, the expanding climate space means that transit costs decrease and thus the impacts of climate change, as modelled here, do not suggest the need for immediate action.

This work supports the need for a more dynamic approach to nature conservation that has been identified by a number of researchers and the role of the landscape matrix in facilitating or hindering species' response to climate change. (Hannah et al., 2002; Midgley et al., 2003; Araújo et al., 2004; Williams et al., 2005).

4.4. Conclusions

The species set used in this work is too limited to draw conclusions of general application and the results should be interpreted with due caution taking into account the limitations of the modelling framework and uncertainties in the climate and land use change scenarios. Nevertheless, two general conclusions seem to consolidate after examining the resulting patterns of response. The first is based on the fact that climate change takes place at several spatial scales simultaneously (Scheffer et al., 2005). The large, zonal patterns imposed by climatic gradients at the continental scale can only be valid in homogeneous territories where local factors have a neutral effect on the concerned species (Breckle, 2002). In all other cases, certainly those included in this study, shorter gradients at more local scales will create a finer texture of fragmentation that will modify the suitability envelope of species, sometimes in situ without an actual displacement of the bulk distribution centroids. The more such smaller gradients can compensate the effect of an unfavourable climate change, the more apparent will be their effect on fragmentation. This is somewhat comparable to the conditions at the edge of a species geographic range, and it can be detected through the uncertainty of the predicted distribution. Thuiller et al. (2003) explored environmental correlates of tree species in northeast Spain, and one of their results was that 'zonal species, or species at the core of their range, were generally well predicted, while extrazonal species, or species at the edge of their range, were predicted only moderately well'. The term extrazonal was suggested by Walter (1970) to describe vegetation beyond the limits of its climatic range and for which the local climate is decisive. If we accept Walter's (1970) definition, it might be proposed that climate change involves the transformation of zonal responses into extrazonal ones.

The second conclusion relates to the fragmentation of suitable space that is associated with climate and land use change, which can be somewhat interpreted as a loss of density of a species' distribution. The results of this paper show shifts or in situ contractions of suitable areas, hence leaving a gap behind. Although none of the models used here deal with complex population dynamics or interactions, it

seems reasonable to assume that such gaps will be opened for colonisation by other species that may be better adapted to the new conditions created by the change. Several studies on the impacts of climate change assume that such a gap will be filled by the next adjacent zonal vegetation. For example, under a climate warming scenario, LeHouerou (1992) predicts that 'xerothermo-Mediterranean and thermo-Mediterranean vegetation, now rare on the northern shores of the Mediterranean, will considerably expand to the foothills of the Apennines, Southern Alps, Cevennes and Pyrenees'.

However, complete replacements can be expected to be very slow, at least from a policy perspective. A conservative estimate can be obtained when the problem is examined by looking backwards in the past. Recent paleoecological studies suggest a time resolution of hundreds or even thousands of years to account for natural climate changes of a magnitude comparable to that of scenarios used here, both in Mediterranean (Goni et al., 2005) and in Boreal (Kullman, 1995) regions. At the opposite end, the process can be initiated very early if a land use change favourable to the replacing species is concurrent, as Penuelas and Boada (2003) reports on a biome shift from *Fagus sylvatica* (beech) to *Q. ilex* in northeast Spain over a few decades. In Britain, forestry is facilitating the spread of *F. sylvatica* into woodlands in suitable northern climate space, as it is widely planted beyond its native range (Berry et al., 2002).

All the zonal types of vegetation involve a certain degree of environmental stability by definition, and this is in turn related to the rate of change of climatic factors. Natural climate change is slow and it can be accompanied by a biologically significant evolutionary response (Davis et al., 2005). But relatively fast changes such as those in the scenarios used in this study imply that climate will be transitional at the time scale of most of the long-lived species. This may reduce their population sizes and result in populations existing in climatic non-equilibrium (Dyer, 1994; Araújo and Pearson, 2005), being unable to migrate into a new potential habitat (Iverson et al., 2004), or losing resilience to the point that a contrasting state is reached (Scheffer et al., 2001). Incidentally, it is interesting to note that the most affected species often form the basis of conservation policies because of their habitat building capacity.

If the previous proposition on the extrazonality of climate change were likely, it follows that in situ changing conditions would maintain the vegetation cover in a permanent transition, and opportunistic species typical of initial secondary successional stages would have a better chance of survival. In short, it might also be proposed that climate change would not involve a zonal shift of natural vegetation, but instead gaps would open within the current vegetation zones and they would be colonised by low quality, early successional species. Only after the change processes were settled (in an ecological time scale, beyond that of human management), could new zonal vegetation be expected.

This work has shown that at the regional scale climate and land use change can both affect the future viability of species. Thus not only is a dynamic, but also an integrated landscape, rather than species or habitat-based, conservation policy required if the impacts of climate change on natural systems are to be mitigated.

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G. del Barrio is a Tenured Scientist in the Desertification and Geocology Group at Estacion Experimental de Zonas Aridas (CSIC). His work on landscape ecology addresses pattern detection in natural vegetation, the use of scale as an indicator of the landscape condition, and the analysis of regional connectivity. Some recent developments include regionalisation of large territories using multivariate analysis of topographic variables, inductive spatial modelling of vegetation and soil thematic maps, field sampling optimisation through analysis of regional stationarity, and the assessment of conservation networks in terms of connectivity and representativity.

P.A. Harrison is a Senior Research Scientist within the Biodiversity Group at the Environmental Change Institute, with more than 15 years experience in the field of climate change impacts on biodiversity and agriculture. Her work focuses on the development and application of mathematical models for crops, species, habitats and ecosystems, including modelling the response of species' distributions to climate change, long-distance dispersal across fragmented landscapes, the impacts of socio-economic and environmental change on managed and natural ecosystems and linking biodiversity models with other sectoral impact models on agricultural land use, water and coastal zones.

P.M. Berry is a Senior Research Scientist and Leader of the Biodiversity Group at the Environmental Change Institute, with more than 12 years experience in the field of climate change impacts on biodiversity. She has considerable expertise on the influence of climate and socio-economic change on plant communities and species' distributions and has been involved in research projects on climate change impacts, landscape dynamics, species modelling, and conservation and biodiversity policy. She has worked extensively with stakeholders in conservation management and policy to define climate change concerns, identify key species and habitats and assess alternative response strategies in relation to European and UK policy.

N. Butt is currently working on her DPhil in tropical climatology and biodiversity at the Oxford University Centre for the Environment. She previously worked for several years in the Biodiversity Group at the Environmental Change Institute researching and modelling the impacts of projected climate change on species' distributions in temperate systems across the UK and Europe. Trained as an ecologist, she subsequently became the computer modeller and climate data manager for the group, contributing to a range of projects investigating climate change impacts and the related conservation and biodiversity policy aspects.

M.E. Sanjuan is a hired scientist within the Desertification and Geocology Group at Estacion Experimental de Zonas Aridas (CSIC). She has expertise in digital cartography and computer models operating with geodatabases. Her current work focuses on the assessment of land condition based on earth observation, and on the application of spatial models to assess the landscape structure.

R.G. Pearson is a postdoctoral fellow at the American Museum of Natural History where he is associated with both the Center for Biodiversity and Conservation and the Department of Herpetology. His research falls principally within the fields of biogeography

and spatial ecology, with a current focus being the development and application of species' distribution (ecological niche) modelling approaches.

T. Dawson is Director of the MSc in Environment and Development, at the Centre for the study of Environmental Change and

Sustainability, University of Edinburgh. He was previously Senior Research Fellow in the Environmental Change Institute, University of Oxford when much of this work was undertaken. His current research interests are in biogeography and climate change and anthropogenic impacts on ecosystems and natural resources, especially on isolated islands.