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3 **Predicting shifts in the climate space of freshwater fishes in Great Britain due to**
4 **climate change**

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6 Ana Ruiz-Navarro, Phillipa K. Gillingham, J. Robert Britton

7 Centre for Ecology, Environment and Sustainability, Department of Life and

8 Environmental Sciences, Bournemouth University, Poole, Dorset BH12 5BB, UK

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10 Corresponding author: Robert Britton, Tel: +44 (0)1202 965384, Email:

11 rbritton@bournemouth.ac.uk

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Abstract

The implications of climate change for terrestrial and aquatic taxa are for their dispersal pole-wards and/ or to higher altitudes as they track their climate niches. Here, bioclimatic models are developed to predict how projected climate change scenarios for a northern temperate region (Great Britain) shift the climate spaces (i.e. areas of suitable thermal habitat) for 12 freshwater fishes of the Salmonidae, Percidae, Esocidae and Cyprinidae families. Climate envelope models developed in Biomod2 used the current species' distributions and their relationships with current climatic variables, and projected these onto the BCC-CSM1-1 and HadGEM2-AO climate change scenarios (low and high emissions, 2050 and 2070) in full and no dispersal scenarios. Substantial contractions in climate spaces were predicted for native salmonid fishes, with decreases of up to 78 % for Atlantic salmon *Salmo salar*, with these largely unchanged between the dispersal scenarios. Conversely, for the majority of cyprinid fishes, expansions were predicted, including into northern regions where they are current not present biogeographically. Only under the no dispersal scenarios did their predicted distributions remain the same as their current distributions. For all non-salmonid species, the most important climate variables in the model predictions related to temperature; for salmonids, they were a combination of temperature and shifts in annual mean precipitation. As these predictions suggest that there is potential for considerable alterations to the climate spaces of freshwater fishes in Great Britain during this century then regulatory and mitigation conservation actions should be undertaken to minimise these.

Introduction

Freshwater environments and their fishes are especially sensitive to the effects of climate change as the persistence and quality of aquatic habitats are strongly reliant on climatic and hydrologic regimes (Morrongiello et al., 2011). The vulnerability of freshwater fish communities to altered climatic patterns is highlighted by their isolation and fragmentation within terrestrial landscapes that typically result in river basins acting as biogeographic islands (Fausch et al., 2002; Gozlan et al., 2010; Olden et al., 2010). This reliance on climate patterns for their thermal regimes and hydrology suggest that they will be particularly vulnerable to changes that result from the alterations in air temperatures and precipitation patterns that are projected to occur during this century (Johnson et al., 2009; Hobday and Lough, 2011).

The predicted effects of climate change on fishes are associated with their thermal tolerances (Rahel and Olden, 2006); where these are due to be either surpassed or optimised for species due to warming then range shifts and expansions can be expected (Graham and Harrod, 2009; Morrongiello et al., 2011; Comte and Grenouillet, 2013, Comte et al., 2013). The species-specific effects of temperature changes on distributions of freshwater fishes are a reflection of the interactions of their changing hydrological and thermal habitats with their physiological and life-history characteristics, and thus potentially result in considerable effects at the species level that will then affect patterns of freshwater biogeography at larger spatial scales (Heino et al., 2009). In general, climate change predictions for both terrestrial and aquatic taxa tend to be for movements pole-wards and/ or to higher altitudes (Chen et

al., 2011; Comte and Grenouillet, 2013; O'Connor et al., 2015), as species attempt to track their climate niches (Crimmins et al., 2011).

In predicting how climate change will alter the distribution of species, bioclimatic envelopes assess the responses of a species to current climatic conditions in order to predict how their distribution will then alter in projected future climate scenarios (Berry et al., 2002; Heikkinen et al., 2006). Bioclimatic envelopes assume that climate is the primary factor determining species' distributions, and that range shifts will occur promptly in response to climate change (Woodward and Beerling, 1997; Hampe, 2004). For freshwater fishes to track their climate niche then they must either be able to disperse through suitable corridors that connect their isolated habitats (Poff et al., 2002) or they will require some managed translocations, a continuing source of debate (e.g. Olden et al., 2010, 2011; Schwartz et al., 2012). Thus, the utility of bioclimatic models for the conservation management of freshwater fishes is arguably their identification of how the areas of suitable thermal habitat available to species (hereafter referred to as their climate space) will alter, highlighting the species and spatial areas of their existing ranges that are most vulnerable to the adverse effects of climate change (Staudt et al., 2013). The identification of the fishes and basins at most risk of alterations in their distribution of their species can then be prioritised for immediate management actions that should then provide the greatest long-term conservation benefits.

The aim of this study was thus to develop bioclimate models to predict how climate change could alter the available climate space for a range of freshwater fishes across a number of families with varying thermal preferences in a northern temperate region

during this century (2050 and 2070). The model region was Great Britain, which has sufficient latitude, longitudinal and altitudinal ranges to provide marked differences in regional climates, and the model fishes were 12 species from across four families of varying thermal tolerances and with strong data on their presence/ absence. It was predicted that the available climate space for each fish species would shift northwards under the modelled climate change scenarios, but the extent of the changes would vary at both species and family levels.

Materials and methods

The modelled fishes were from the families Salmonidae (*Salmo trutta*, *Salmo salar*), Percidae (*Perca fluviatilis*), Esocidae (*Esox lucius*) and Cyprinidae (*Cyprinus carpio*, *Carassius carassius*, *Scardinius erythrophthalmus*, *Rutilus rutilus*, *Squalius cephalus*, *Abramis brama*, *Leuciscus leuciscus* and *Gobio gobio*). For the latter five species of the Cyprinidae family, data were reported initially in Ruiz-Navarro et al. (2016). However, their model predictions are included here in order to provide comprehensive comparisons across the four fish families and to present some new results from the models. Where the data from in Ruiz-Navarro et al. (2016) for these five cyprinid fishes are used in the Results, this original source has been cited appropriately.

As the 12 fishes were selected on the basis of their conservation, recreational and/ or socio-economic importance, this meant that species without these interests, such as minnow *Phoxinus phoxinus* and stone loach *Barbatula barbatula*, were not modelled. The modelled fishes included species with preferences for relatively cold waters (<

15°C, e.g. *S. salar*, *S. trutta*), cool waters ($\leq 20^{\circ}\text{C}$, e.g. *R. rutilus*, *S. erythrophthalmus*) and relatively warm waters ($> 20^{\circ}\text{C}$, e.g. *C. carpio*) (Rahel and Olden, 2006; www.Fishbase.org). Other than *C. carpio*, all of the modelled species have native ranges in Great Britain. Due to their non-native status, *C. carpio* would normally not be suitable for climate modelling using the methodology outlined below, as they do not have a natural biogeographic range in Great Britain. However, their introduction history means they are considered naturalised in parts of Britain (primarily England) and have attained a widespread distribution during the last 100 years that suggests they are now present in all regions that are climatically suitable for their persistence (Britton et al., 2010).

Within the bioclimate models, data on the occurrences of the fishes within Great Britain were obtained from the ‘Database for the Atlas of Freshwater Fishes’, provided by the Biological Records Centre, available at the NBN Gateway website (<https://data.nbn.org.uk/Datasets/GA000174>). The majority of the records ranged from 1950 to 2003 in the British National Grid spatial reference system (based on the 1936 Ordnance Survey Great Britain datum, OSGB_36) at a 10 x 10 km resolution. They represent an accumulation of the recordings of each species over time within these grid squares and so all of the data were utilised in the models. The British National Grid spatial references were then converted to the World Geodetic System WGS_84 grid system so that the occurrence data matched the available climatic data. Species absences were considered to be sampled locations in Great Britain where fish species other than the fishes were present in the ‘Database for the Atlas of Freshwater Fishes’, i.e. squares that have not been visited by fish recorders were not considered for use in the modelling (Ruiz-Navarro et al., 2016).

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143 The climate data utilised baseline (1950-2000) and future global projections of
144 climate data (annual values) obtained from the WorldClim website
145 (<http://www.worldclim.org/>, Hijmans et al., 2005), version 1.4 (release 3), at a 5-min
146 resolution in the WGS_84 grid system. Climate projections for the years 2050 and
147 2070, under low (rcp 2.6) and high (rcp 8.5) emission scenarios were obtained from
148 two different climate prediction models: BCC-CSM1-1 and HadGEM2-AO. BCC-
149 CSM1-1 was produced by the Beijing Climate Center, China Meteorological
150 Administration, whereas the Hadley Centre of the Meteorological Office of the UK
151 produced HadGEM2-AO. The use of projections from both climate models thus
152 provides 8 climate change scenarios for application to the bioclimate models and so a
153 wider range of modelled scenarios than if only one climate model was used.

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155 A 'UK outline polygon', obtained from the OS Opendata website
156 (<https://www.ordnancesurvey.co.uk/opendatadownload/products.html>), was used to
157 clip the climatic data to the area of Great Britain. The 19 climatic variables available,
158 derived from the monthly temperature and rainfall values, were reduced to six through
159 analysis of their correlations so that only variables with low pairwise correlations
160 were used in the models (Dormann et al., 2013). This was completed through use of
161 Pearson's correlation coefficient, with a threshold of $r = 0.70$ used to remove highly
162 correlated variables from the climate data set (Ruiz-Navarro et al. 2016). As a result,
163 the climatic variables used were: annual mean temperature (°C), mean diurnal range
164 of temperature (°C), isothermality ($100 * (\text{mean diurnal range} / \text{annual range of}$
165 $\text{temperature}))$, mean temperature of wettest quarter (°C), mean temperature of driest
166 quarter (°C), and annual precipitation (mm). The rationale for retaining these variables

rather than their correlates was because they represent the two primary properties of the climate, energy and water that tend to be physiologically limiting factors for aspects of the biology and ecology of ectotherms, such as fish (Chu et al. 2005). It is, however, acknowledged that these climate variables are not the only determinants of fish distribution (Pont *et al.*, 2006), with a range of other abiotic and biotic variables also often being important parameters that it was not possible to model here (Ruiz-Navarro et al., 2016).

Fish species distributions in Great Britain were modelled using seven algorithms available in the *biomod2* package (Thuiller *et al.*, 2014) in R: (1) generalized linear models (GLM), (2) generalized additive models (GAM), (3) multivariate adaptive regression splines (MARS), (4) classification tree analysis (CTA), (5) boosted regression trees (BRT), (6) random forests (RF), and (7) artificial neural networks. In all models, the default options of *biomod2* were selected, with the exception of restricting the GAM smoothing to 4 knots to avoid over-fitting the data. Evaluation of the models was through the area under the ROC curve (AUC), using an 80:20 split of training to test data and 50 evaluation repetitions. AUC values range between 0 and 1, where 1 indicates excellent model performance and values lower than 0.5 indicate predictive discrimination that is no better than a random guess (Ruiz-Navarro et al., 2016). Marmion et al. (2009) outlined that the usefulness and accuracy of bioclimate models for conservation, i.e. their robustness, were improved when ‘consensus’ models were used, i.e. ensemble models. This was because ensemble models overcome the variability of predictions that can occur between single models. Thus, ensemble models were created in *biomod2* by weighting the single models by their AUC score, with only single models that had individual AUC evaluation scores of \geq

0.7 included in the calculation. Where a single model had an AUC evaluation score below this then it would be excluded from the ensemble.

For the ensemble model of each species, the importance of the included climate predictors (i.e. annual mean temperature, mean diurnal range of temperature, isothermality, mean temperature of wettest quarter, mean temperature of driest quarter and annual precipitation) were then determined using the variables importance function, with the importance values converted to proportions (%) to facilitate their interpretation. These were run 10 times per species, with their mean (\pm SE) calculated.

Once the probability of presence of each species had been estimated for each geographic grid square by the ensemble models, a threshold of probability of presence was then applied to the cells. There are a number of options for selecting this threshold, including use of the threshold probability that maximises kappa and thus minimises prediction error based on current climate conditions (e.g. Huntley *et al.*, 2008). However, models that have high probability thresholds (e.g. 0.8) tend to be less good at generalising than models of low probability thresholds (e.g. 0.5), although use of the latter increases the chance of prediction error (Liu *et al.*, 2005). Consequently, whilst thresholds of 0.5, 0.6 and 0.8 were tested initially, a threshold of 0.6 was selected for final use. The decision to use 0.6 across all models and species was based on the trade-offs between model generality and prediction error (Liu *et al.*, 2005; Ruiz-Navarro *et al.*, 2016).

Following the application of this threshold of probability of presence, the number of grid squares that were predicted to be occupied by each species was then counted for the different scenarios, and the location of the corresponding centroids was calculated. The ensemble models were then evaluated using the ROC curve (AUC), which is used extensively in species distribution modelling (SDM) (Elith *et al.*, 2006), and it is generally considered the best metric for comparisons in the same geographic space (Buisson *et al.*, 2008). The centroids of the simulated present ranges and the predicted future climate spaces of each species in each climate change projection were then calculated as the points about which the sum of the distances of all the grid squares in which the species was predicted to be present was zero, with the Euclidean distances from all cells to the centroid calculated and then tested for differences from the predicted centroid under the current conditions.

The model outputs were then compared between the different predictions under scenarios. The first was maximum dispersal, achieved in the model by enabling the predictions for each species to be projected across all of Great Britain. Thus, this represented a scenario where the species were free to move within Britain and thus track their climate niche fully. It was calculated as all of the squares in the new predicted range. The second was no dispersal of each species, achieved in the model by restricting predictions to the current range. Thus, this represented a scenario where each species was unable to move from its current distribution. It was calculated as the number of squares in the new predicted range that overlapped with the original predicted range. The modelling architecture did not allow for any other dispersal scenarios, for example, dispersal opportunities within and between catchments. The maximum dispersal scenario thus acknowledges that whilst the climate space of the

species might be predicted to alter with a changing climate, this does not necessarily mean this will occur due to extant dispersal opportunities. Consequently, the outputs from the distribution-climate modelling of the fishes for each climate change projection was the simulated extent of the spatial area of Great Britain that populations of these fishes in current climate conditions (see Online Appendix 1,2), their distribution under minimum and maximum dispersal scenarios, and the climate variables contributing most to the predictions.

Results

The ensemble models predicting the distributions of the fishes included all of the individual models that were initially considered, as their AUC values were higher than 0.7 in all cases. All ensemble models had AUC values of ≥ 0.91 and, with the exception of *S. trutta* (0.49) had kappa values ≥ 0.64 (Table 1). The highest root mean squared error value was 0.44 (*P. fluviatilis*; Table 1).

The ensemble models predicted that the climate space of the two salmonid fishes in Great Britain would constrict under all projected climate change scenarios, with predicted declines of up to 56 % for *S. trutta* and 78 % for *S. salar* (Table 2; Fig. 1; Online Appendix 1,2). This shift in their climate space, as revealed by the direction and distance of centroid displacement, was displacement in a north-westerly direction of between 130 and 243 km for *S. trutta* and 78 to 293 km for *S. salar* (Table 3; Fig. 2). The largest displacements were under the high emission scenarios of the HadGEM2-AO predictions. If there were no opportunities for the species to disperse from their current distribution, then considerable declines in their current distribution

were predicted, particularly in the high emission scenario of HadGEM2-AO in 2070 (-56 % for *S. trutta* and -83 % for *S. salar*) (Table 4). However, even if these fishes have the opportunity to disperse to rivers where they are not currently present, the extent of their distribution decline will still be similar to no dispersal due to their current wide spatial distribution (Table 4). These two fishes were the only species where annual mean precipitation was an important variable contributing to the model predictions, with it being the most important variable for *S. trutta* (Table 5). For *S. salar*, the most important predictor was annual mean temperature (49.9 %; Table 5).

The climate spaces of *P. fluviatilis* and *E. Lucius* in Great Britain were predicted to expand, with increases of between 35 and 62 %, and 37 and 67 % respectively (Table 2; Online Appendix 1,2). Whilst the shifts in these distributions were also predicted to be in a north-westerly direction, these were comparatively low when compared with the salmonids, with predicted shifts of between 40 and 78 km for *P. fluviatilis* and 13 and 49 km for *E. lucius* (Table 3; Fig. 2). By contrast, if there were no dispersal opportunities from their existing ranges for both species, predictions were for no change to their current distribution (Table 4). For both fishes, annual mean temperature and mean diurnal range of temperature were the most important climatic variables contributing to their predictions, totalling 84.2 % for *E. lucius* and 90.2 % for *P. fluviatilis*.

The outputs of the ensemble models for the cyprinid fishes revealed varying predictions, with some species predicted to undergo considerable expansions in their climate spaces, including *S. erythrophthalmus* (77 to 177 %), *R. rutilus* (44 to 88 %) and *A. brama* (80 to 143 %) (Table 2; Online Appendix 1,2), with centroid

291 displacements all in a north-westerly direction (*S. erythrophthalmus*: 29 to 115 km; *R.*
 292 *rutilus*: 75 to 121 km; *A. brama*: 54 to 117 km; Table 3; Ruiz-Navarro et al., 2016).
 293 Predictions for *C. carpio* were an expanded climate space of between 68 and 136 %,
 294 with centroid displacement of between 64 and 105 km (Table 2, 3; Fig. 2, 3). For *S.*
 295 *cephalus*, climate space constriction of between 19 and 82 % was predicted (Table 2),
 296 with centroid displacement of up to 398 km (Table 3; Fig. 2) (Ruiz-Navarro et al.,
 297 2016). For *C. carassius*, *L. leuciscus* and *G. gobio*, predictions varied with the
 298 projected climate change scenario, covering both climate space expansion and
 299 constriction depending on the climate change scenario (Table 2, 3; Fig. 2; Online
 300 Appendix 1,2). For *C. carassius*, expansions were generally predicted under high
 301 emissions and constriction under some low emissions, with the converse for *L.*
 302 *leuciscus* and *G. gobio* (Table 2, 3; Online Appendix 1,2; Ruiz-Navarro et al., 2016).
 303
 304 These climate niche predictions were also reflected in their dispersal predictions; for
 305 species whose climate niches were predicted to expand (Table 3), such as *R. rutilus*
 306 and *C. carpio*, there would be no change in their current range if there were no
 307 dispersal opportunities available (Table 4). Under full dispersal opportunities, their
 308 distributions would increase given their predicted increases in climate niche (Table 4).
 309 For species where predictions for their climate niches were decreases, then there was
 310 a general predicted decrease in their distribution under no dispersal, but this was
 311 lessened under full dispersal (Table 4). For *S. cephalus* and *G. gobio* under no
 312 dispersal and high emission scenarios for 2070, some predictions were for extinction
 313 from Britain, highlighting the importance of dispersal opportunities for some species
 314 to persist (Table 4). Annual mean temperature was the most important climatic
 315 variable in the model predictions of the cyprinid fishes, ranging from 47.9 % for *C.*

carassius to 71.7 % for *L. leuciscus* (Table 5). Its importance for *C. carpio* was also relatively high (70.3 %). The combined importance of annual mean temperature and mean diurnal range of temperature ranged between 61.6 and 94.4 % across the species (Table 5).

Discussion

Building bioclimate models for a range of freshwater fishes in Great Britain under current and future climate scenarios predicted that the climate space of each species would shift, with centroid displacement always in a north-westerly direction. Predictions revealed that even under low emission climate change scenarios and the two dispersal scenarios, alterations in climate space were generally consistent at the family level, with constriction for the freshwater life-stages of native salmonid fishes and a large increase in the climate space of most cyprinid species, including the non-native *C. carpio*, other than under the no dispersal scenario when their distribution would be unchanged. Across all the modelled fishes, annual mean temperature was the most important variable in the ensemble model predictions. There was, however, some inter-family variability across the importance of the climatic variables, with a combination of annual mean precipitation and temperature variables being most important for the two salmonid species. For all other modelled species, temperature variables were most important, with their combined importance to the ensemble models being a minimum of 92 %. The limitation of the modelling architecture to the use of only two dispersal scenarios limited the distribution predictions to scenarios of no dispersal and full dispersal. It is highly probable that some dispersal within and between some catchments of species will occur naturally and/ or by anthropogenic

means (Conti et al., 2015). This is thus a limitation of the method used and so it is recommended that future work incorporates the ability of freshwater fish to disperse in relation to hydrological connectivity and the changes in their environments.

The modelling approach was based on bioclimatic variables, using the assumption that the influence of climate on the biology and ecology of the fishes was the key determinant of their distribution pattern (Woodward and Beerling, 1997; Hampe, 2004). It is important, therefore, to also acknowledge other factors that could also have influenced these distributions. The strength of competitive interactions between species might alter under the new conditions and also potentially lead to novel interactions, thus impacting community structure and thus species' distributions (Van Zuiden et al., 2015). Where species such as *C. carpio* establish, their ability to increase water turbidity through foraging might adversely impact the persistence of sight feeding piscivores such as *E. lucius* (Matsuzaki et al., 2007, 2009). Long-term changes in the abiotic and biotic characteristics of British freshwaters include river impoundments, including weir construction impacting migration (especially in the 1900s) (Higgs & Petts, 1988), chronic pollution, impacting nutrient loading and eutrophication (Amisah & Cowx, 2000), and changes in land-use and agricultural practises, altering riparian vegetation (Johnes, 1996; Whitehead et al., 2002). Whilst all these extant issues can profoundly alter fish communities, their impacts in Britain mainly affect fish abundance, community structure and life history traits (e.g. Beardsley & Britton 2013), rather than presence/ absence. We thus suggest that bio-climate relationships remain an important component in determining freshwater fish distributions in Britain, especially for the species that were modelled.

The assumption that the bioclimate models were suitable for use in the study was supported by their predictions being highly consistent with those from other fish-based climate change studies. These generally provide strong evidence from both freshwater and marine systems that range changes will occur in most fishes due to climate change (Jackson & Mandrak, 2002; Chu *et al.*, 2005; Rahel & Olden, 2008; Jones *et al.*, 2013; Elliott *et al.*, 2015). Whilst the direction and magnitude of range shifts are shaped by the species-specific sensitivity to the changes (e.g. their physiological tolerance, resilience and potential to adapt) (Graham & Harrod, 2009; Comte & Grenouillet, 2015), the general pattern over a wide range of terrestrial and aquatic taxa is a pole-ward and altitudinal range shift as species track their thermal niche (e.g. Chen *et al.*, 2011; Melles *et al.*, 2011), including plants (Corlett & Westcott, 2013) and insects (Forister *et al.*, 2010). The drivers of these range changes can be complex, with Conti *et al.* (2015) suggesting that where species had expanding ranges, this was influenced more by changes in the seasonality of temperatures, whereas where ranges contract, it is due to the interaction of temperature change and alterations in precipitation patterns. Indeed, the importance of annual mean precipitation and temperature variables for the predicted range contractions of the salmonids was consistent with this. For *G. gobio* and *L. leuciscus*, predictions suggested some temperature thresholds might exist, given their predicted expansions of climate space under low emission projections of climate space but constrictions under high emissions.

The predicted constrictions in the climate space of the salmonid species, especially under high emission scenarios, were consistent with them being ‘cold-water’ fishes with relatively low thermal optima (Rahel and Olden, 2006). Across their global

range, there are substantial concerns for the long-term persistence of salmonid fishes in many regions (e.g. Chu et al., 2005; Battin et al., 2007; Ficke et al., 2007; Almodóvar et al., 2012). Nevertheless, in Great Britain, the projected changes in their climate spaces suggest that even in high emission scenarios there are likely to be some rivers at northern latitudes where sustainable populations are able to survive. However, their populations further south are likely to be under considerable threat and where populations could persist, such as in some upland rivers in Southwest England, studies suggest there will be considerable shifts in their biology and ecology due to the combination of increasing temperatures and shifts in precipitation patterns. For example, Jonsson and Jonsson (2009) predicted that for both *S. salar* and *S. trutta*, their traits of age at first maturity, longevity and fecundity would decrease with increasing temperatures. Should changing temperature and rainfall patterns shift the timing of smolt migration to earlier in the year, there could be implications for their marine survival, as smolts in cohorts that emigrate later tend to have increased sea survival rates (Kennedy and Crozier 2010). Whilst Elliott and Elliott (2010) predicted that *S. trutta* growth could benefit from small increases in temperature ($< 2.5^{\circ}\text{C}$), increases of more than 3°C could result in negative growth consequences. Jensen et al. (2008) suggested, however, that *S. trutta* populations are likely to have some potential for adapting to changing temperature regimes. In combination, this suggests some persistence in native salmonid populations might be evident in Britain under projected climate changes, but their life histories traits and migration strategies will be altered, and they could potentially have lower sea survival.

The predicted range changes for the cyprinid fishes varied by species, but most had increased climate space, with this space shifting into regions into northern and

western Britain where they are not currently present. Only under a scenario of no dispersal did the predicted future distribution of most species match that of their current distribution. These predictions, where mean annual temperature was the most important climatic variable in all cases, were also consistent with other studies and aligned to these fishes often preferring warmer waters to salmonids. For example, they were consistent with those of Graham and Harrod (2009) and Elliot et al. (2015), who both highlighted that species such as *R. rutilus* in Great Britain would be strongly favoured under climate change, with potential for invasions into non-indigenous areas. Of arguably greater concern were, however, the predictions for *C. carpio*, a fish typically considered as preferring water temperatures above 20 °C (Britton et al., 2007). This fish is already recognised as invasive globally (e.g. Koehn 2004; Zambrano et al., 2006; Britton et al., 2007). Their range in Great Britain is already widespread, being present in the majority of river catchments in England following their high stocking pressure into lake fisheries and their subsequent escape during floods (Britton et al. 2010). This should be a conservation and ecological concern, as under favourable thermal conditions the species is highly invasive (Smith and Walker, 2004; Oyugi et al., 2011), with impacts including substantial declines of submerged vegetation (Williams et al., 2002; Britton et al., 2007) and the re-suspension of sediments that increase water turbidity (Lougheed et al., 2004; Matsuzaki et al., 2007, 2009).

In many cases, the projected rapidity of projected change will exceed the ability of species to adapt or disperse to more climatically favorable surroundings. This has resulted in debate over the appropriateness of managed relocations (MR) of species to locations where their future persistence may be more probable (e.g. Lawler & Olden,

2011; Pérez et al., 2012; Klenk & Larson, 2013). Olden et al. (2010) argued that due to the constrained existence of freshwater organisms within highly dendritic networks, MR should represent a useful conservation strategy, but with the caveat that the properties of freshwaters also increases the probability of unintended ecological consequences. They concluded that species with a high probability of unintended effects to recipient ecosystems should not be used in MR (Olden et al. 2010). These conclusions have potentially high applicability to the results of the bioclimate models presented here. These suggested that a range of conservation measures is required across the modeled species. These include the prevention of translocation and invasion of *C. carpio*, *R. rutilus* and *S. erythrophthalmus* in northern latitudes, such as via regulatory measures (Hickley & Chare, 2004; Winfield et al., 2010). They also include conserving climate-vulnerable species, such as *S. trutta*, and *S. salar*. Where their local populations become extirpated due to climate change then MR could be considered if efforts are taken to reduce temperature and precipitation impacts, with the latter likely to relate to low flow issues in summer months (Johnson et al., 2009). The MR would then ideally use fish from the same basin to avoid potential genetic issues (Griffiths et al., 2009).

Should MR be argued as an undesirable conservation action for salmonid fishes in Britain, allied to the full dispersal predictions indicating similar decreases in distribution to the no dispersal predictions, then alternative conservation measures would be required. In areas predicted to be on the edge or outside of the future climate space of these fishes, such as many areas of central and southern England, the current *in situ* conservation management ought to shift away from strategies that are often strongly reliant on stocking rivers with juvenile life stages of hatchery reared fish,

especially for *S. salar* (Aprahamian et al., 2003, 2004). Instead, they should focus on physical changes that seek to maintain habitat quantity and quality under low flow scenarios and minimise the concomitant warming of water temperatures as air temperatures increase. For example, Broadmeadow et al. (2011) revealed that increasing levels of riparian woodland prevented water temperatures exceeding lethal limits for *S. trutta* in streams of the New Forest, Southern England via shading, with 20 to 40 % shading of the channel effective at preventing thermal limits being reached and 80 % shading maintaining the thermal optima for *S. trutta* somatic growth (Broadmeadow et al., 2011). Whilst alterations in riparian shading could have substantial consequences for the trophic interactions of the salmonid populations (e.g. Dineen et al., 2007), it nevertheless could provide considerable ‘proofing’ against warming that would otherwise result in river temperatures exceeding safe thermal limits. This would then also provide considerable conservation benefits for other threatened freshwater species that will be climate-change stressed, such as white-clawed crayfish *Austropotamobius pallipes* (Capinha et al., 2013). Other possibilities could be to attempt to increase food supply and/ or reduce predation pressure, both of which have been postulated as promising methods for maintaining the European Golden Plover *Pluvialis apricaria* under moderate climatic change (Pearce-Higgins, 2011).

In conclusion, there were considerable predicted alterations in the climate spaces of the modelled freshwater fishes in Great Britain. Use of two dispersal scenarios (minimum and maximum) indicated the extent of the potential changes in their distributions. Some caution in their interpretation is warranted in relation to the actuality of their distributions shifting in accordance with these, and they overlook

other, non-climate related factors (such as other abiotic factors) and interactions that also influence current distributions and future alterations. Nevertheless, the utility of these models for conservation management is in highlighting the species that are at risk of causing invasions in new locations where dispersal opportunities exist, whether these are natural or anthropogenic. For these species, regulatory and remediation actions should minimise this risk. The models also highlighted that for the modelled salmonid fishes, *in situ* habitat management can be used to minimise the detrimental impacts of climate change on their distributions, given that MR is unlikely to be successful given the predictions of decreases under the full dispersal scenario. Thus, these models should facilitate a range of management and regulatory tools to be either maintained or implemented across Great Britain that increase the probability of salmonid populations persisting in southern and western regions, and avoid invasions of cyprinid species across northern regions.

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Table 1. Number of 10 x 10 km squares currently occupied in Great Britain by each species and the performance metrics of the ensemble distribution models per species. Area under the curve (AUC), Cohen’s kappa coefficient (Kappa) and root mean squared error (RMSE).

| Family | Species | Current squares | AUC | Kappa | RMSE |
|------------|----------------------------------|--------------------|-------|-------|-------|
| Salmonidae | <i>S. trutta</i> | 2435 | 0.923 | 0.487 | 0.295 |
| | <i>S. salar</i> | 1503 | 0.917 | 0.671 | 0.408 |
| Percidae | <i>P. fluviatilis</i> | 1121 | 0.907 | 0.637 | 0.439 |
| Esocidae | <i>E. lucius</i> | 1066 | 0.905 | 0.650 | 0.429 |
| Cyprinidae | <i>C. carassius</i> | 174 | 0.927 | 0.619 | 0.356 |
| | <i>S. erythrophthalmus</i> | 547 | 0.925 | 0.657 | 0.388 |
| | <i>R. rutilus</i> ¹ | 1073 | 0.954 | 0.758 | 0.348 |
| | <i>S. cephalus</i> ¹ | 801 | 0.947 | 0.703 | 0.373 |
| | <i>A. brama</i> ¹ | 796 | 0.944 | 0.706 | 0.357 |
| | <i>L. leuciscus</i> ¹ | 785 | 0.945 | 0.697 | 0.373 |
| | <i>G. gobio</i> ¹ | 894 | 0.942 | 0.700 | 0.363 |
| | <i>C. carpio</i> | 909 | 0.933 | 0.676 | 0.377 |

¹Data presented in Ruiz-Navarro et al. (2016)

Table 2. Grade of change (%) in the number of squares occupied by the species for each projected future scenario. Low ES: low emissions scenario; High ES: high emissions scenario. (See Online appendix 1 for full table including changes in the numbers of occupied squares).

| | Year | BCC-CSM1-1 | | HadGEM2-AO | | Source |
|----------------------------|------|------------|---------|------------|---------|----------------------------|
| | | Low ES | High ES | Low ES | High ES | |
| <i>S. trutta</i> | 2050 | -32.20 | -41.31 | -35.81 | -40.83 | This study |
| | 2070 | -30.31 | -56.27 | -29.34 | -53.15 | |
| <i>S. salar</i> | 2050 | -42.33 | -58.35 | -52.20 | -65.92 | This study |
| | 2070 | -47.67 | -71.60 | -44.69 | -78.09 | |
| <i>P. fluviatilis</i> | 2050 | 35.13 | 48.66 | 61.53 | 65.69 | This study |
| | 2070 | 38.30 | 48.17 | 58.35 | 72.62 | |
| <i>E. lucius</i> | 2050 | 37.01 | 49.23 | 67.09 | 66.50 | This study |
| | 2070 | 38.38 | 49.23 | 60.85 | 75.73 | |
| <i>C. carassius</i> | 2050 | -28.57 | 65.80 | 123.81 | 184.20 | This study |
| | 2070 | -43.51 | 45.24 | 119.26 | 294.59 | |
| <i>S. erythrophthalmus</i> | 2050 | 76.78 | 122.81 | 119.54 | 134.15 | This study |
| | 2070 | 84.15 | 130.74 | 108.61 | 177.60 | |
| <i>R. rutilus</i> | 2050 | 44.45 | 58.23 | 67.42 | 73.31 | Ruiz-Navarro et al. (2016) |
| | 2070 | 46.71 | 58.75 | 63.26 | 84.23 | |
| <i>S. cephalus</i> | 2050 | -42.20 | -72.25 | -18.54 | -38.75 | Ruiz-Navarro et al. (2016) |
| | 2070 | -19.82 | -82.23 | -2.30 | -77.75 | |
| <i>A. brama</i> | 2050 | 79.93 | 106.94 | 108.18 | 124.41 | Ruiz-Navarro et al. (2016) |
| | 2070 | 89.10 | 113.88 | 95.91 | 143.37 | |
| <i>L. leuciscus</i> | 2050 | 6.33 | -9.61 | -18.52 | -30.13 | Ruiz-Navarro et al. (2016) |
| | 2070 | 15.59 | -46.66 | 6.10 | -88.39 | |
| <i>G. gobio</i> | 2050 | -4.19 | -54.07 | -18.33 | -44.68 | Ruiz-Navarro et al. (2016) |
| | 2070 | 24.89 | -64.48 | 11.43 | -91.40 | |

| | | | | | | |
|------------------|------|-------|--------|--------|--------|------------|
| <i>C. carpio</i> | 2050 | 67.74 | 100.24 | 101.79 | 118.93 | This study |
| | 2070 | 77.62 | 102.74 | 87.26 | 135.60 | |

Table 3. Location (latitude and longitude, decimal degrees) of the centroids of the original distribution of the model fishes and predicted changes in projected emission scenarios (ES) (km, and bearing in arc degrees considering 0° the north and increasing values in a clockwise direction).

(a) BCC-CSM1-1

| Species | Original | | year | Distance | Low ES | | | Distance | High ES | | |
|--------------------------------|-----------|-----------|------|----------|---------------------|--------------------|---------|----------|---------------------|--------------------|---------|
| | Long | Lat | | | Lat (t) | Long(t) | Bearing | | Lat (t) | Long(t) | Bearing |
| <i>S. trutta</i> | -2.905277 | 54.228347 | 2050 | 146 | -15.67 ² | 15.58 ² | 339.2 | 174 | -18.66 ² | 16.93 ² | 341.0 |
| | | | 2070 | 136 | -14.72 ² | 14.33 ² | 339.4 | 225 | -23.56 ² | 16.80 ² | 344.5 |
| <i>S. salar</i> | -3.590507 | 54.913361 | 2050 | 84 | -6.76 ² | 11.65 ² | 334.1 | 86 | -5.34 ² | 14.71 ² | 325.2 |
| | | | 2070 | 78 | -5.88 ² | 11.88 ² | 331.9 | 114 | -6.86 ² | 11.27 ² | 340.8 |
| <i>P. fluviatilis</i> | -1.758949 | 53.144356 | 2050 | 40 | -5.35 ² | 0.79 | 355.5 | 62 | -8.02 ² | 3.91 ² | 345.4 |
| | | | 2070 | 57 | -7.54 ² | 1.89 | 352.3 | 63 | -8.15 ² | 3.63 ² | 346.7 |
| <i>E. lucius</i> | -1.818006 | 53.338692 | 2050 | 13 | -1.64 | -0.48 | 8.8 | 32 | -3.91 ² | 1.61 | 347.8 |
| | | | 2070 | 33 | -4.11 ² | 0.09 | 359.3 | 33 | -4.10 ² | 1.36 | 350.2 |
| <i>C. carassius</i> | -1.026232 | 52.539497 | 2050 | 93 | 11.21 ² | -5.64 ² | 158.2 | 44 | 6.08 ² | 0.61 | 184.4 |
| | | | 2070 | 58 | 5.67 ² | 0.93 | 186.6 | 60 | 8.24 ² | 1.07 | 186.0 |
| <i>S. erythrophthalmus</i> | -1.169132 | 52.52853 | 2050 | 29 | -3.46 ² | 3.64 ² | 323.8 | 68 | -7.31 ² | 9.81 ² | 317.0 |
| | | | 2070 | 41 | -5.27 ² | 4.20 ² | 330.9 | 71 | -7.57 ² | 10.49 ² | 316.1 |
| <i>R. rutilus</i> ³ | -1.497009 | 52.777101 | 2050 | 75 | -10.50 ¹ | 5.40 ¹ | 343.8 | 97 | -13.20 ¹ | 8.60 ¹ | 340.1 |
| | | | 2070 | 89 | -12.40 ¹ | 6.10 ¹ | 344.6 | 101 | -13.70 ¹ | 8.60 ¹ | 340.8 |

| | | | | | | | | | | | |
|----------------------------------|-----------|-----------|------|-----|---------------------|--------------------|-------|-----|---------------------|--------------------|-------|
| <i>S. cephalus</i> ³ | -1.262286 | 52.510828 | 2050 | 178 | -16.60 ¹ | 12.00 ¹ | 344.4 | 361 | -37.50 ¹ | 28.40 ¹ | 343.2 |
| | | | 2070 | 175 | -19.07 ¹ | 15.70 ¹ | 340.3 | 370 | -38.50 ¹ | 26.10 ¹ | 343.1 |
| <i>A. brama</i> ³ | -1.185012 | 52.599898 | 2050 | 74 | -9.91 ¹ | 6.40 ¹ | 338.4 | 102 | -13.50 ¹ | 10.00 ¹ | 335.9 |
| | | | 2070 | 89 | -12.13 ¹ | 7.50 ¹ | 339.4 | 112 | -14.90 ¹ | 10.80 ¹ | 336.7 |
| <i>L. leuciscus</i> ³ | -1.228179 | 52.467966 | 2050 | 59 | -8.20 ¹ | -2.80 ¹ | 11.7 | 95 | -12.00 ¹ | 0.01 | 359.9 |
| | | | 2070 | 76 | -11.25 ¹ | -1.40 ¹ | 4.3 | 168 | -16.90 ¹ | 4.40 ¹ | 352.6 |
| <i>G. gobio</i> ³ | -1.286165 | 52.534677 | 2050 | 135 | -17.60 ¹ | 2.70 ¹ | 355.1 | 245 | -21.80 ¹ | 9.80 ¹ | 347.6 |
| | | | 2070 | 108 | -15.40 ¹ | 2.50 ¹ | 354.6 | 244 | -19.80 ¹ | 9.90 ¹ | 347.2 |
| <i>C. carpio</i> | -1.286484 | 52.552294 | 2050 | 64 | -8.76 ² | 3.72 ² | 345.4 | 101 | -13.55 ² | 8.40 ² | 339.4 |
| | | | 2070 | 78 | -10.71 ² | 5.05 ² | 343.8 | 105 | -14.05 ² | 8.68 ² | 339.6 |

(b) HadGEM2-AO

| Species | Original | | year | Distance | Low ES | | | Distance | High ES | | |
|--------------------------------|-----------|-----------|------|----------|---------------------|--------------------|---------|----------|---------------------|--------------------|---------|
| | Long | Lat | | | Lat (t) | Long(t) | Bearing | | Lat (t) | Long(t) | Bearing |
| <i>S. trutta</i> | -2.905277 | 54.228347 | 2050 | 168 | -18.53 ² | 16.35 ² | 341.0 | 195 | -21.89 ² | 17.51 ² | 342.3 |
| | | | 2070 | 130 | -13.59 ² | 15.90 ² | 336.3 | 243 | -26.88 ² | 20.67 ² | 342.5 |
| <i>S. salar</i> | -3.590507 | 54.913361 | 2050 | 170 | -13.29 ² | 15.42 ² | 340.4 | 236 | -19.18 ² | 17.88 ² | 342.5 |
| | | | 2070 | 145 | -11.14 ² | 15.75 ² | 337.2 | 293 | -26.39 ² | 22.71 ² | 340.4 |
| <i>P. fluviatilis</i> | -1.758949 | 53.144356 | 2050 | 56 | -6.74 ² | 6.86 ² | 330.8 | 65 | -7.86 ² | 7.71 ² | 332.0 |
| | | | 2070 | 50 | -5.99 ² | 6.37 ² | 329.4 | 78 | -9.31 ² | 8.92 ² | 333.1 |
| <i>E. lucius</i> | -1.818006 | 53.338692 | 2050 | 35 | -3.41 ² | 5.47 ² | 319.4 | 38 | -3.93 ² | 5.52 ² | 323.3 |
| | | | 2070 | 29 | -2.55 ² | 5.03 ² | 313.0 | 49 | -5.05 ² | 7.04 ² | 323.9 |
| <i>C. carassius</i> | -1.026232 | 52.539497 | 2050 | 47 | 5.05 ² | 5.89 ² | 222.4 | 50 | -4.62 ² | 6.83 ² | 313.7 |
| | | | 2070 | 44 | 4.35 ² | 5.84 ² | 226.4 | 112 | -11.67 ² | 13.15 ² | 322.7 |
| <i>S. erythrophthalmus</i> | -1.169132 | 52.52853 | 2050 | 52 | -3.00 ² | 9.91 ² | 292.0 | 74 | -7.93 ² | 10.93 ² | 316.0 |
| | | | 2070 | 45 | -1.31 | 8.99 ² | 280.7 | 115 | -13.27 ² | 14.99 ² | 323.0 |
| <i>R. rutilus</i> ³ | -1.497009 | 52.777101 | 2050 | 84 | -10.92 ² | 10.60 ² | 330.5 | 99 | -12.93 ² | 11.80 ² | 332.4 |
| | | | 2070 | 77 | -9.99 ² | 9.93 ² | 329.5 | 121 | -15.73 ² | 13.86 ² | 334.0 |

| | | | | | | | | | | | |
|----------------------------------|-----------|-----------|------|-----|---------------------|--------------------|-------|-----|---------------------|--------------------|-------|
| <i>S. cephalus</i> ³ | -1.262286 | 52.510828 | 2050 | 265 | -32.42 ² | 23.85 ² | 340.0 | 342 | -38.97 ² | 30.54 ² | 341.0 |
| | | | 2070 | 168 | -21.14 ² | 19.60 ² | 332.9 | 398 | -38.30 ² | 30.34 ² | 341.0 |
| <i>A. brama</i> ³ | -1.185012 | 52.599898 | 2050 | 70 | -7.97 ² | 11.11 ² | 317.6 | 93 | -11.55 ² | 12.81 ² | 325.2 |
| | | | 2070 | 54 | -5.36 ² | 9.87 ² | 308.2 | 117 | -14.55 ² | 15.14 ² | 327.7 |
| <i>L. leuciscus</i> ³ | -1.228179 | 52.467966 | 2050 | 177 | -21.92 ² | 3.63 ² | 354.3 | 219 | -22.13 ² | 9.65 ² | 347.6 |
| | | | 2070 | 95 | -13.85 ² | 2.64 ² | 353.0 | 336 | -13.37 ² | 4.27 ² | 350.2 |
| <i>G. gobio</i> ³ | -1.286165 | 52.534677 | 2050 | 226 | -28.69 ² | 12.37 ² | 345.6 | 291 | -28.82 ² | 15.28 ² | 345.1 |
| | | | 2070 | 138 | -19.35 ² | 9.75 ² | 342.1 | 505 | -35.30 ² | 28.22 ² | 344.4 |
| <i>C. carpio</i> | -1.286484 | 52.552294 | 2050 | 72 | -8.79 ² | 9.45 ² | 325.2 | 97 | -12.45 ² | 11.20 ² | 330.7 |
| | | | 2070 | 48 | -5.00 ² | 8.20 ² | 311.1 | 117 | -14.79 ² | 13.42 ² | 331.1 |

¹p≤0.05; ²p≤0.01

³(Ruiz-Navarro et al., 2016)

Table 4. Grade of change (%) in the number of squares occupied by the species for each projected future scenario under full and no dispersal scenarios. Low ES: low emissions scenario; High ES: high emissions scenario. (See Online appendix 1 for full table including changes in the numbers of occupied squares).

(a) BCC-CSM1-1

| Species | Prediction year | Full dispersal | | No dispersal | |
|----------------------------|-----------------|----------------|------------|--------------|------------|
| | | Change (%) | Change (%) | Change (%) | Change (%) |
| <i>S. trutta</i> | 2050 | -37 | -45 | -37 | -45 |
| | 2070 | -35 | -59 | -35 | -59 |
| <i>S. salar</i> | 2050 | -43 | -59 | -44 | -59 |
| | 2070 | -49 | -72 | -49 | -72 |
| <i>P. fluviatilis</i> | 2050 | 48 | 63 | 0 | 0 |
| | 2070 | 51 | 62 | -1 | 0 |
| <i>E. lucius</i> | 2050 | 50 | 64 | -1 | 0 |
| | 2070 | 52 | 64 | -2 | 0 |
| <i>C. carassius</i> | 2050 | 90 | 340 | -45 | -41 |
| | 2070 | 50 | 286 | -48 | -44 |
| <i>S. erythrophthalmus</i> | 2050 | 137 | 198 | 0 | 0 |
| | 2070 | 146 | 209 | 0 | 0 |
| <i>R. rutilus</i> | 2050 | 55 | 70 | 0 | 0 |
| | 2070 | 58 | 71 | 0 | 0 |
| <i>S. cephalus</i> | 2050 | -44 | -73 | -71 | -100 |
| | 2070 | -22 | -83 | -65 | -100 |
| <i>C. carpio</i> | 2050 | 77 | 111 | 0 | 0 |
| | 2070 | 87 | 114 | 0 | 0 |
| <i>A. brama</i> | 2050 | 85 | 113 | 0 | 0 |
| | 2070 | 94 | 120 | 0 | 0 |
| <i>L. leuciscus</i> | 2050 | 1 | -14 | -21 | -40 |
| | 2070 | 10 | -49 | -19 | -69 |
| <i>G. gobio</i> | 2050 | -7 | -55 | -41 | -84 |
| | 2070 | 21 | -65 | -21 | -87 |

(b) HadGEM2-AO

| Species | Prediction year | Full dispersal | | No dispersal | |
|----------------------------|-----------------|----------------|------------|--------------|------------|
| | | Change (%) | Change (%) | Change (%) | Change (%) |
| <i>S. trutta</i> | 2050 | -40 | -45 | -40 | -45 |
| | 2070 | -34 | -56 | -34 | -56 |
| <i>S. salar</i> | 2050 | -53 | -66 | -54 | -67 |
| | 2070 | -46 | -78 | -47 | -83 |
| <i>P. fluviatilis</i> | 2050 | 77 | 81 | 0 | 0 |
| | 2070 | 73 | 89 | 0 | 0 |
| <i>E. lucius</i> | 2050 | 83 | 83 | 0 | -1 |
| | 2070 | 77 | 93 | -1 | -1 |
| <i>C. carassius</i> | 2050 | 494 | 655 | -37 | -10 |
| | 2070 | 482 | 948 | -39 | -9 |
| <i>S. erythrophthalmus</i> | 2050 | 194 | 213 | 0 | 0 |
| | 2070 | 179 | 271 | 0 | 0 |
| <i>R. rutilus</i> | 2050 | 80 | 86 | 0 | 0 |
| | 2070 | 76 | 98 | 0 | 0 |
| <i>S. cephalus</i> | 2050 | -20 | -40 | -85 | -97 |
| | 2070 | -5 | -78 | -61 | -100 |
| <i>C. carpio</i> | 2050 | 113 | 131 | 0 | 0 |
| | 2070 | 98 | 149 | 0 | 0 |
| <i>A. brama</i> | 2050 | 114 | 131 | 0 | 0 |
| | 2070 | 101 | 150 | 0 | 0 |
| <i>L. leuciscus</i> | 2050 | -22 | -33 | -60 | -76 |
| | 2070 | 1 | -89 | -69 | -97 |
| <i>G. gobio</i> | 2050 | -21 | -46 | -73 | -89 |
| | 2070 | 8 | -92 | -46 | -100 |

Table 5. Importance of each climatic variable, expressed as proportion of the total importance (%), in the ensemble model predictions of the shifts in climate space per species, with the overall mean provided per climatic variable. AMT: annual mean temperature; MDRT: mean diurnal range of temperature; IT: isothermality; MTWQ: mean temperature of wettest quarter; MTDQ: mean temperature of driest quarter; and AP: annual precipitation

| Species | Proportion of model prediction explained by climatic variable (%) | | | | | |
|----------------------------|---|----------------|---------------|---------------|---------------|---------------|
| | AMT | MDRT | IT | MTWQ | MTDQ | AP |
| <i>S. trutta</i> | 23.8 | 8.6 | 3.2 | 24.4 | 6.3 | 33.7 |
| <i>S. salar</i> | 49.9 | 10.5 | 2.9 | 1.6 | 1.2 | 34.0 |
| <i>P. fluviatilis</i> | 43.5 | 46.7 | 1.6 | 0.5 | 2.4 | 5.2 |
| <i>E. lucius</i> | 30.7 | 53.5 | 3.5 | 1.7 | 2.7 | 8.0 |
| <i>C. carassius</i> | 47.9 | 13.7 | 2.3 | 4.1 | 27.5 | 4.5 |
| <i>S. erythrophthalmus</i> | 65.8 | 17.9 | 5.3 | 1.9 | 4.5 | 4.6 |
| <i>R. rutilus</i> | 58.3 | 34.4 | 1.4 | 0.2 | 3.1 | 2.6 |
| <i>S. cephalus</i> | 61.2 | 33.2 | 0.7 | 0.8 | 2.8 | 1.3 |
| <i>C. carpio</i> | 70.3 | 20.0 | 0.6 | 0.7 | 6.3 | 2.1 |
| <i>A. brama</i> | 68.2 | 23.9 | 0.5 | 0.8 | 3.5 | 3.2 |
| <i>L. leuciscus</i> | 71.7 | 19.6 | 1.3 | 1.2 | 1.5 | 4.7 |
| <i>G. gobio</i> | 70.6 | 23.7 | 1.2 | 0.8 | 2.0 | 1.7 |
| Mean (\pm SE) | 55.2 \pm 4.7 | 25.5 \pm 4.0 | 2.0 \pm 0.4 | 3.2 \pm 1.9 | 5.3 \pm 2.1 | 8.8 \pm 3.4 |

Figure captions

Figure 1. Current spatial distribution of Atlantic salmon *Salmo salar* in Great Britain (left) and their predicted climate space under BCC-CSM1-1 low emission scenario in 2050 (middle) and high emission in 2070 (right). On the predicted maps, colours represent the probability (0 to 1) of species presence in the climate change projection, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0.

Figure 2. The extent of centroid displacement, all in a generally north-westerly direction, for (A) *Esox lucius* (clear cross), *Perca fluviatilis* (black cross), *Salmo salar* (filled circle) and *Salmo trutta* (clear circle); (B) *Gobio gobio* (clear cross), *Rutilus rutilus* (black cross), *Squalius cephalus* (filled circle) and *Leuciscus leuciscus* (clear circle); and (C) *Scardinius erythrophthalmus* (clear cross), *Carassius carassius* (black cross), *Abramis brama* (filled circle) and *Cyprinus carpio* (clear circle).

Figure 3. Current spatial distribution of Common carp *Cyprinus carpio* in Great Britain (left) and their predicted climate space under BCC-CSM1-1 low emission scenario in 2050 (middle) and high emission in 2070 (right). On the predicted maps, colours represent the probability (0 to 1) of species presence in the climate change projection, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0.

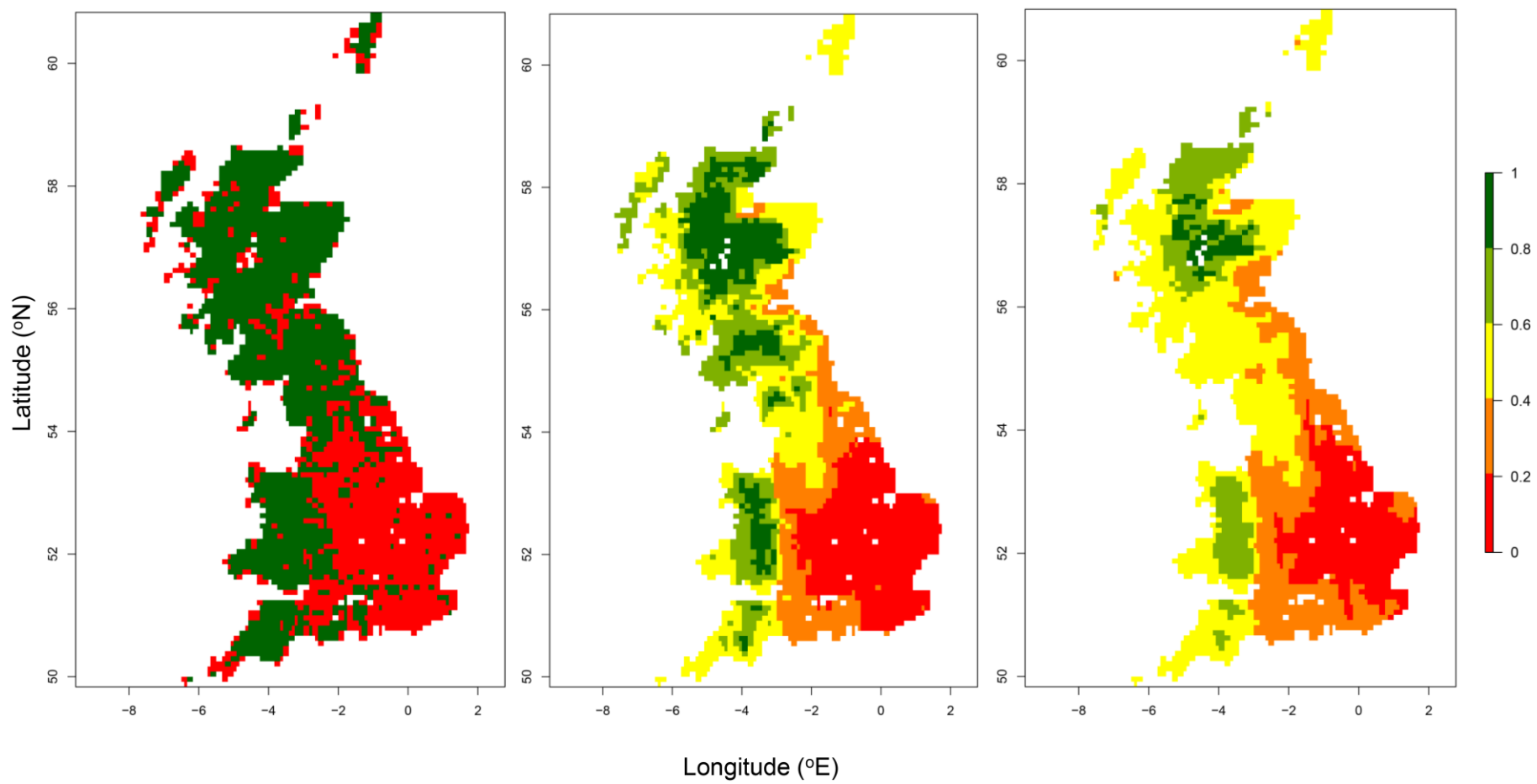


Figure 1.

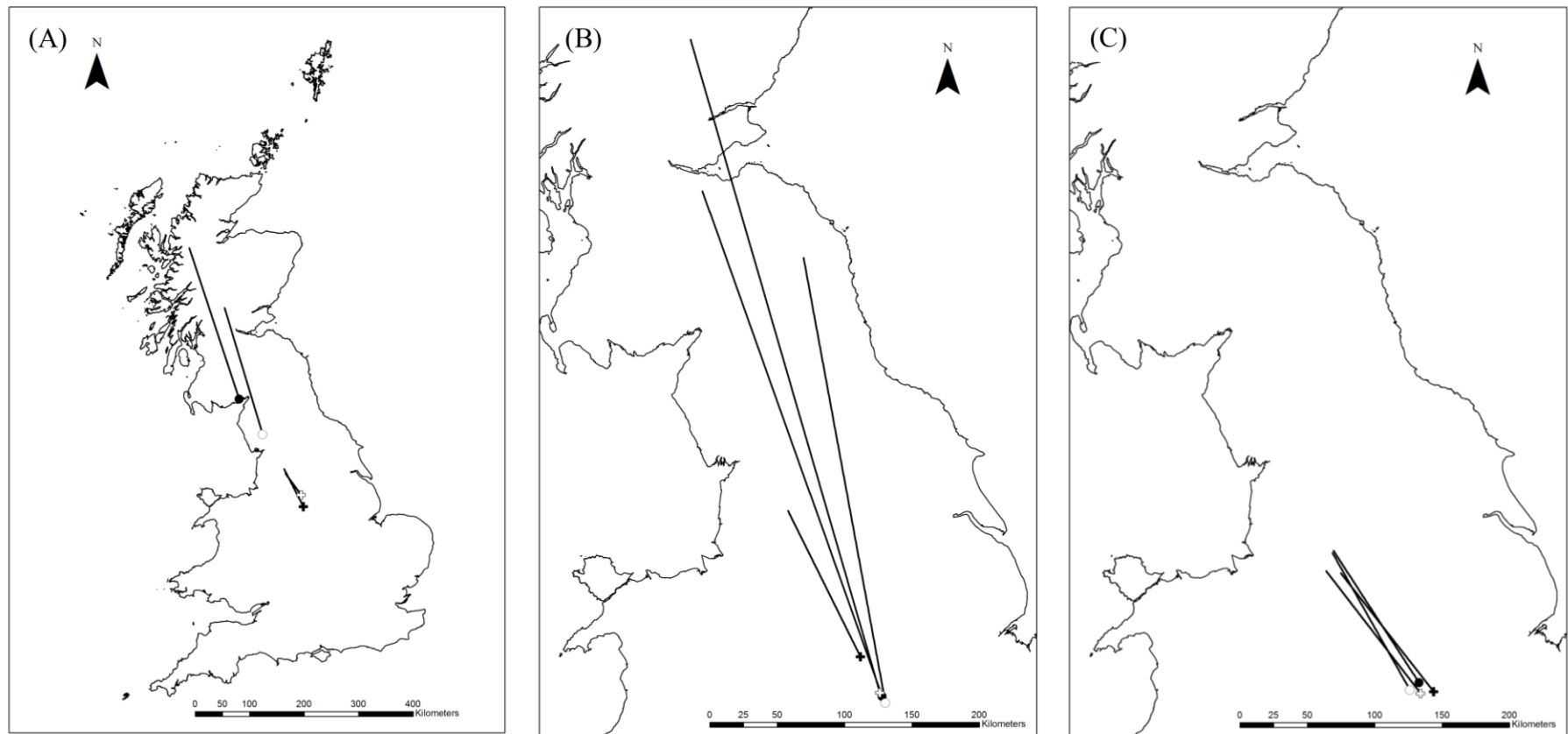


Figure 2.

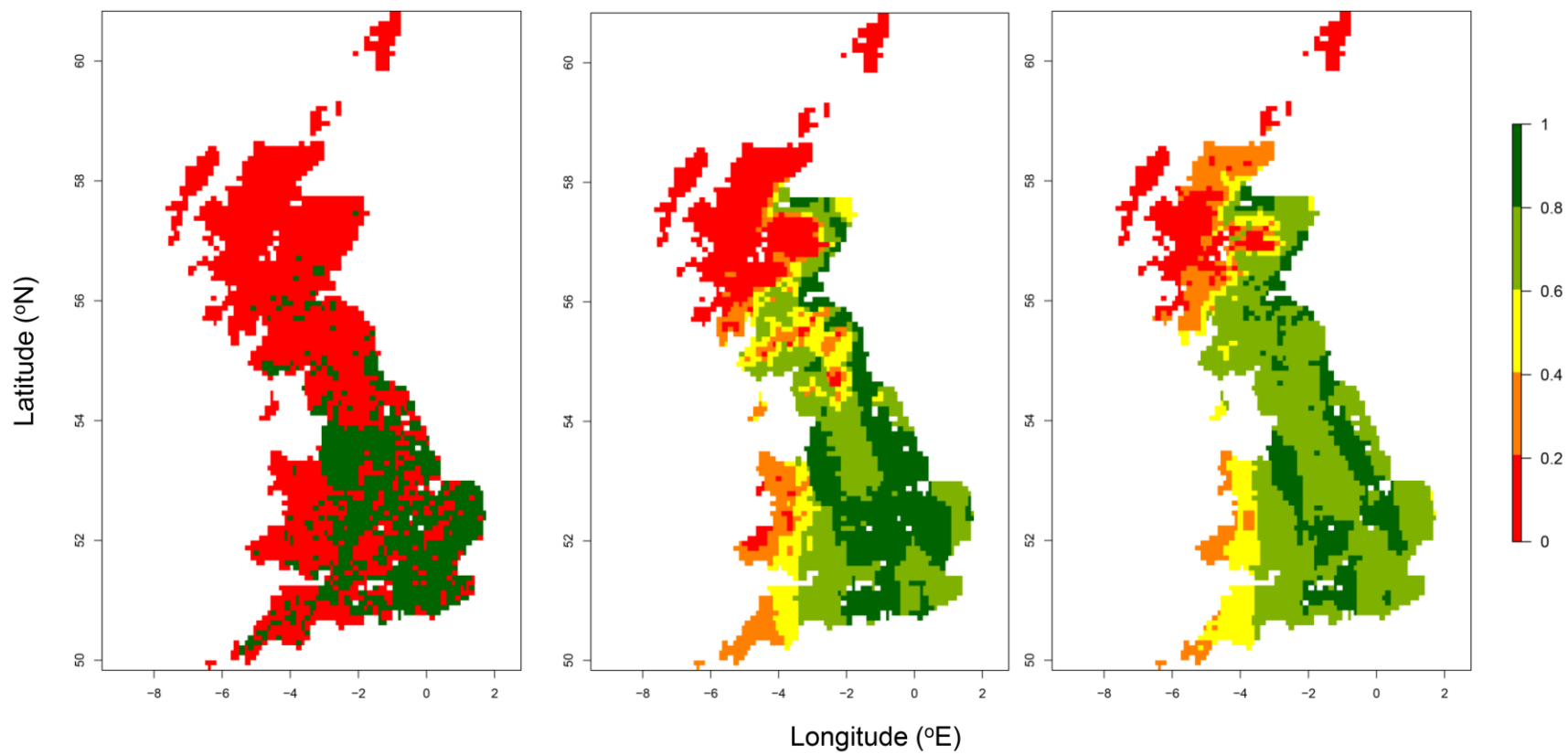


Figure 3.

Online appendices

Table A1. Number of actual squares occupied by the species at present (original) and in the projected future scenarios, and grade of change (%) respect to the original distribution. Low ES: low emissions scenario; High ES: high emissions scenario. (*cf.* Table 2 in main paper)

| | Original | BCC-CSM1-1 | | | | | HadGEM2-AO | | | | Source |
|----------------------------|----------|-------------|--------|-------------|---------|-------------|------------|-------------|---------|-------------|------------|
| | | Prediction | Low ES | | High ES | | Low ES | | High ES | | |
| | | No. squares | year | No. squares | Change | No. squares | Change | No. squares | Change | No. squares | |
| <i>S. trutta</i> | 2273 | 2050 | 1541 | -32.20 | 1334 | -41.31 | 1459 | -35.81 | 1345 | -40.83 | This study |
| | | 2070 | 1584 | -30.31 | 994 | -56.27 | 1606 | -29.34 | 1065 | -53.15 | |
| <i>S. salar</i> | 1479 | 2050 | 853 | -42.33 | 616 | -58.35 | 707 | -52.20 | 504 | -65.92 | This study |
| | | 2070 | 774 | -47.67 | 420 | -71.60 | 818 | -44.69 | 324 | -78.09 | |
| <i>P. fluviatilis</i> | 1227 | 2050 | 1658 | 35.13 | 1824 | 48.66 | 1982 | 61.53 | 2033 | 65.69 | This study |
| | | 2070 | 1697 | 38.30 | 1818 | 48.17 | 1943 | 58.35 | 2118 | 72.62 | |
| <i>E. lucius</i> | 1170 | 2050 | 1603 | 37.01 | 1746 | 49.23 | 1955 | 67.09 | 1948 | 66.50 | This study |
| | | 2070 | 1619 | 38.38 | 1746 | 49.23 | 1882 | 60.85 | 2056 | 75.73 | |
| <i>C. carassius</i> | 462 | 2050 | 330 | -28.57 | 766 | 65.80 | 1034 | 123.81 | 1313 | 184.20 | This study |
| | | 2070 | 261 | -43.51 | 671 | 45.24 | 1013 | 119.26 | 1823 | 294.59 | |
| <i>S. erythrophthalmus</i> | 732 | 2050 | 1294 | 76.78 | 1631 | 122.81 | 1607 | 119.54 | 1714 | 134.15 | This study |
| | | 2070 | 1348 | 84.15 | 1689 | 130.74 | 1527 | 108.61 | 2032 | 177.60 | |

| | BCC-CSM1-1 | | | | | | HadGEM2-AO | | | | |
|----------------------------|-------------|------------|-------------|--------|-------------|--------|-------------|--------|-------------|--------|------------|
| | Original | Prediction | Low ES | | High ES | | Low ES | | High ES | | |
| | No. squares | year | No. squares | Change | No. squares | Change | No. squares | Change | No. squares | Change | |
| <i>Rutilus rutilus</i> | 1154 | 2050 | 1667 | 44.45 | 1826 | 58.23 | 1932 | 67.42 | 2000 | 73.31 | 1 |
| | | 2070 | 1693 | 46.71 | 1832 | 58.75 | 1884 | 63.26 | 2126 | 84.23 | |
| <i>Squalius cephalus</i> | 782 | 2050 | 452 | -42.20 | 217 | -72.25 | 637 | -18.54 | 479 | -38.75 | 1 |
| | | 2070 | 627 | -19.82 | 139 | -82.23 | 764 | -2.30 | 174 | -77.75 | |
| <i>Abramis brama</i> | 807 | 2050 | 1452 | 79.93 | 1670 | 106.94 | 1680 | 108.18 | 1811 | 124.41 | 1 |
| | | 2070 | 1526 | 89.10 | 1726 | 113.88 | 1581 | 95.91 | 1964 | 143.37 | |
| <i>Leuciscus leuciscus</i> | 853 | 2050 | 907 | 6.33 | 771 | -9.61 | 695 | -18.52 | 596 | -30.13 | 1 |
| | | 2070 | 986 | 15.59 | 455 | -46.66 | 905 | 6.10 | 99 | -88.39 | |
| <i>Gobio gobio</i> | 884 | 2050 | 847 | -4.19 | 406 | -54.07 | 722 | -18.33 | 489 | -44.68 | 1 |
| | | 2070 | 1104 | 24.89 | 314 | -64.48 | 985 | 11.43 | 76 | -91.40 | |
| <i>C. carpio</i> | 840 | 2050 | 1409 | 67.74 | 1682 | 100.24 | 1695 | 101.79 | 1839 | 118.93 | This study |
| | | 2070 | 1492 | 77.62 | 1703 | 102.74 | 1573 | 87.26 | 1979 | 135.60 | |

1: Data presented in Ruiz-Navarro et al. (2016)

Table A2. Number of squares predicted as occupied by the species at present (Original) versus those in the projected future scenarios under full and no dispersal scenarios and their grade of change (%) with respect to the original predicted distribution. Low ES: low emissions scenario; High ES: high emissions scenario. (*cf.* Table 4 in main paper).

(a) BCC-CSM1-1

| Species | Current (Predicted squares) | Prediction year | Full dispersal | | | | No dispersal | | | |
|----------------------------|-----------------------------------|-----------------|---------------------|---------------|----------------------|---------------|---------------------|---------------|----------------------|---------------|
| | | | Low ES (squares) | Change (%) | High ES (squares) | Change (%) | Low ES (squares) | Change (%) | High ES (squares) | Change (%) |
| <i>S. trutta</i> | 2435 | 2050 | 1541 | -37 | 1334 | -45 | 1541 | -37 | 1334 | -45 |
| | | 2070 | 1584 | -35 | 994 | -59 | 1584 | -35 | 994 | -59 |
| <i>S. salar</i> | 1503 | 2050 | 853 | -43 | 616 | -59 | 849 | -44 | 615 | -59 |
| | | 2070 | 774 | -49 | 420 | -72 | 773 | -49 | 420 | -72 |
| <i>P. fluviatilis</i> | 1121 | 2050 | 1658 | 48 | 1824 | 63 | 1121 | 0 | 1121 | 0 |
| | | 2070 | 1697 | 51 | 1818 | 62 | 1113 | -1 | 1121 | 0 |
| <i>E. lucius</i> | 1066 | 2050 | 1603 | 50 | 1746 | 64 | 1059 | -1 | 1066 | 0 |
| | | 2070 | 1619 | 52 | 1746 | 64 | 1048 | -2 | 1066 | 0 |
| <i>C. carassius</i> | 174 | 2050 | 330 | 90 | 766 | 340 | 95 | -45 | 102 | -41 |
| | | 2070 | 261 | 50 | 671 | 286 | 91 | -48 | 97 | -44 |
| <i>S. erythrophthalmus</i> | 547 | 2050 | 1294 | 137 | 1631 | 198 | 547 | 0 | 547 | 0 |
| | | 2070 | 1348 | 146 | 1689 | 209 | 547 | 0 | 547 | 0 |
| <i>R. rutilus</i> | 1073 | 2050 | 1667 | 55 | 1826 | 70 | 1073 | 0 | 1070 | 0 |
| | | 2070 | 1693 | 58 | 1832 | 71 | 1072 | 0 | 1070 | 0 |
| <i>S. cephalus</i> | 801 | 2050 | 452 | -44 | 217 | -73 | 231 | -71 | 1 | -100 |
| | | 2070 | 627 | -22 | 139 | -83 | 280 | -65 | 0 | -100 |
| <i>C. carpio</i> | 796 | 2050 | 1409 | 77 | 1682 | 111 | 796 | 0 | 793 | 0 |
| | | 2070 | 1492 | 87 | 1703 | 114 | 796 | 0 | 793 | 0 |
| <i>A. brama</i> | 785 | 2050 | 1452 | 85 | 1670 | 113 | 785 | 0 | 785 | 0 |
| | | 2070 | 1526 | 94 | 1726 | 120 | 785 | 0 | 785 | 0 |
| <i>L. leuciscus</i> | 894 | 2050 | 907 | 1 | 771 | -14 | 706 | -21 | 540 | -40 |
| | | 2070 | 986 | 10 | 455 | -49 | 728 | -19 | 276 | -69 |
| <i>G. gobio</i> | 909 | 2050 | 847 | -7 | 406 | -55 | 534 | -41 | 146 | -84 |
| | | 2070 | 1104 | 21 | 314 | -65 | 718 | -21 | 122 | -87 |

(b) HadGEM2-AO

| Species | Current (squares) | Prediction year | Full dispersal | | | | No dispersal | | | |
|----------------------------|----------------------|--------------------|---------------------|---------------|----------------------|---------------|---------------------|---------------|----------------------|---------------|
| | | | Low ES (squares) | Change (%) | High ES (squares) | Change (%) | Low ES (squares) | Change (%) | High ES (squares) | Change (%) |
| <i>S. trutta</i> | 2435 | 2050 | 1459 | -40 | 1345 | -45 | 1459 | -40 | 1345 | -45 |
| | | 2070 | 1606 | -34 | 1065 | -56 | 1606 | -34 | 1065 | -56 |
| <i>S. salar</i> | 1503 | 2050 | 707 | -53 | 504 | -66 | 696 | -54 | 496 | -67 |
| | | 2070 | 818 | -46 | 324 | -78 | 800 | -47 | 259 | -83 |
| <i>P. fluviatilis</i> | 1121 | 2050 | 1982 | 77 | 2033 | 81 | 1121 | 0 | 1121 | 0 |
| | | 2070 | 1943 | 73 | 2118 | 89 | 1121 | 0 | 1121 | 0 |
| <i>E. lucius</i> | 1066 | 2050 | 1955 | 83 | 1948 | 83 | 1063 | 0 | 1053 | -1 |
| | | 2070 | 1882 | 77 | 2056 | 93 | 1052 | -1 | 1056 | -1 |
| <i>C. carassius</i> | 174 | 2050 | 1034 | 494 | 1313 | 655 | 110 | -37 | 156 | -10 |
| | | 2070 | 1013 | 482 | 1823 | 948 | 107 | -39 | 159 | -9 |
| <i>S. erythrophthalmus</i> | 547 | 2050 | 1607 | 194 | 1714 | 213 | 547 | 0 | 547 | 0 |
| | | 2070 | 1527 | 179 | 2032 | 271 | 547 | 0 | 547 | 0 |
| <i>R. rutilus</i> | 1073 | 2050 | 1932 | 80 | 2000 | 86 | 1073 | 0 | 1073 | 0 |
| | | 2070 | 1884 | 76 | 2126 | 98 | 1073 | 0 | 1073 | 0 |
| <i>S. cephalus</i> | 801 | 2050 | 637 | -20 | 479 | -40 | 124 | -85 | 21 | -97 |
| | | 2070 | 764 | -5 | 174 | -78 | 313 | -61 | 0 | -100 |
| <i>C. carpio</i> | 796 | 2050 | 1695 | 113 | 1839 | 131 | 796 | 0 | 796 | 0 |
| | | 2070 | 1573 | 98 | 1979 | 149 | 796 | 0 | 796 | 0 |
| <i>A. brama</i> | 785 | 2050 | 1680 | 114 | 1811 | 131 | 785 | 0 | 785 | 0 |
| | | 2070 | 1581 | 101 | 1964 | 150 | 785 | 0 | 785 | 0 |
| <i>L. leuciscus</i> | 894 | 2050 | 695 | -22 | 596 | -33 | 359 | -60 | 212 | -76 |
| | | 2070 | 905 | 1 | 99 | -89 | 276 | -69 | 24 | -97 |
| <i>G. gobio</i> | 909 | 2050 | 722 | -21 | 489 | -46 | 246 | -73 | 101 | -89 |
| | | 2070 | 985 | 8 | 76 | -92 | 490 | -46 | 0 | -100 |

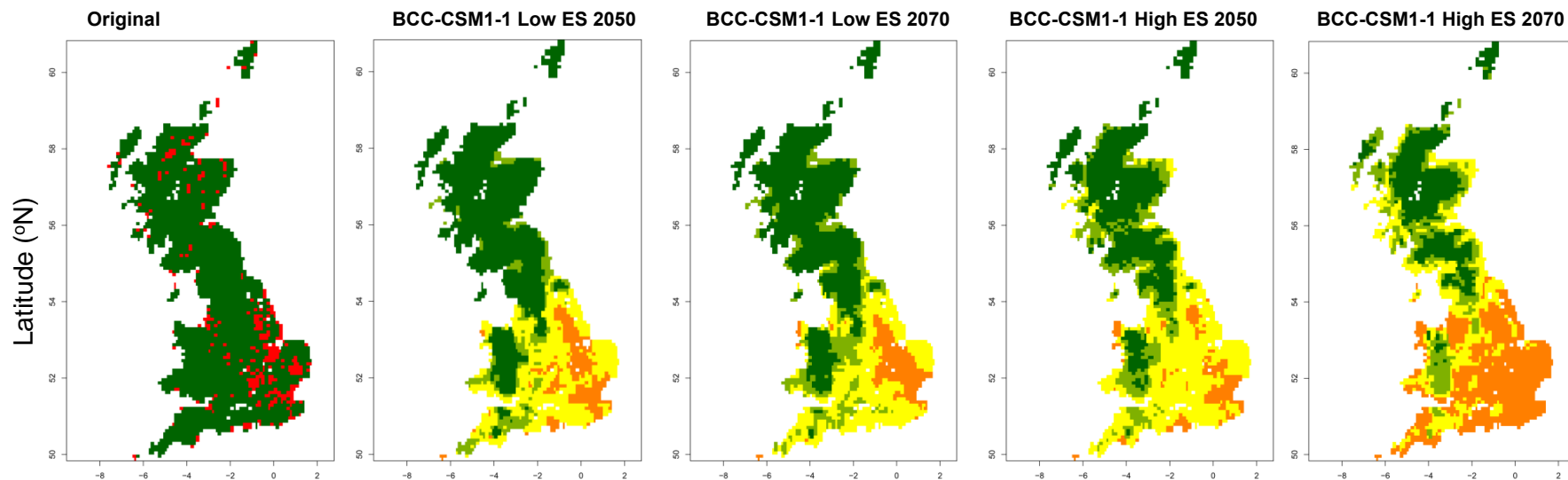
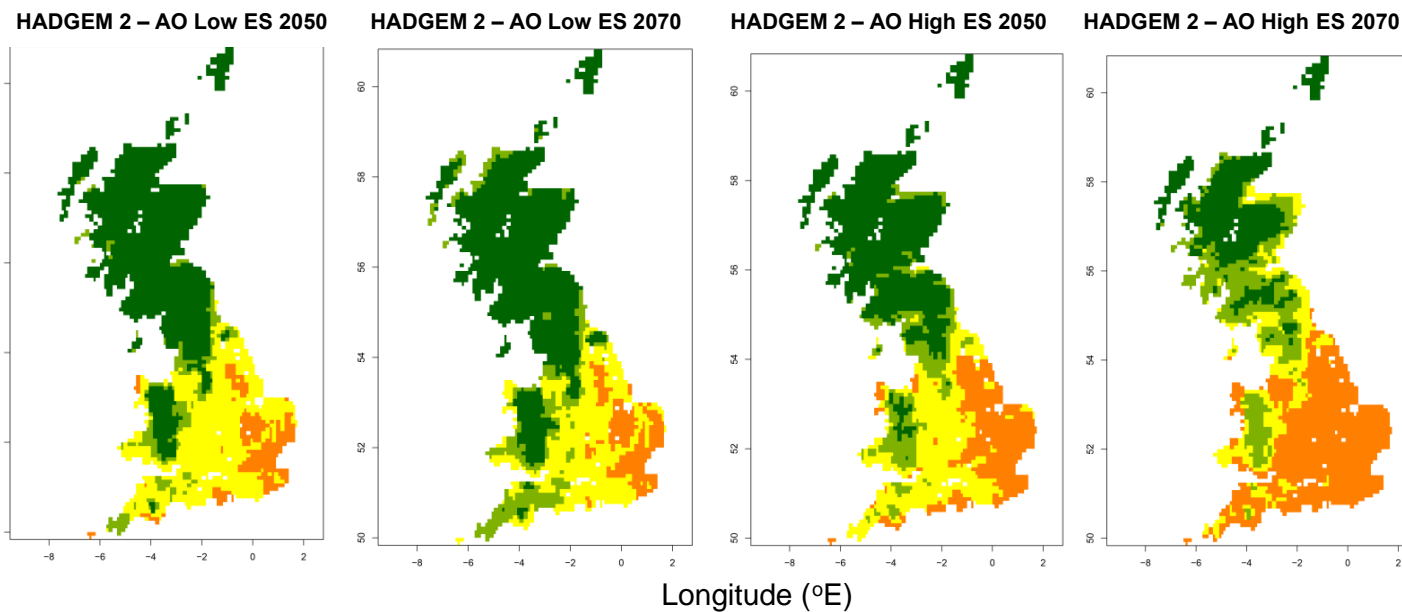


Figure A1.

Climate space of *Salmo trutta* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0



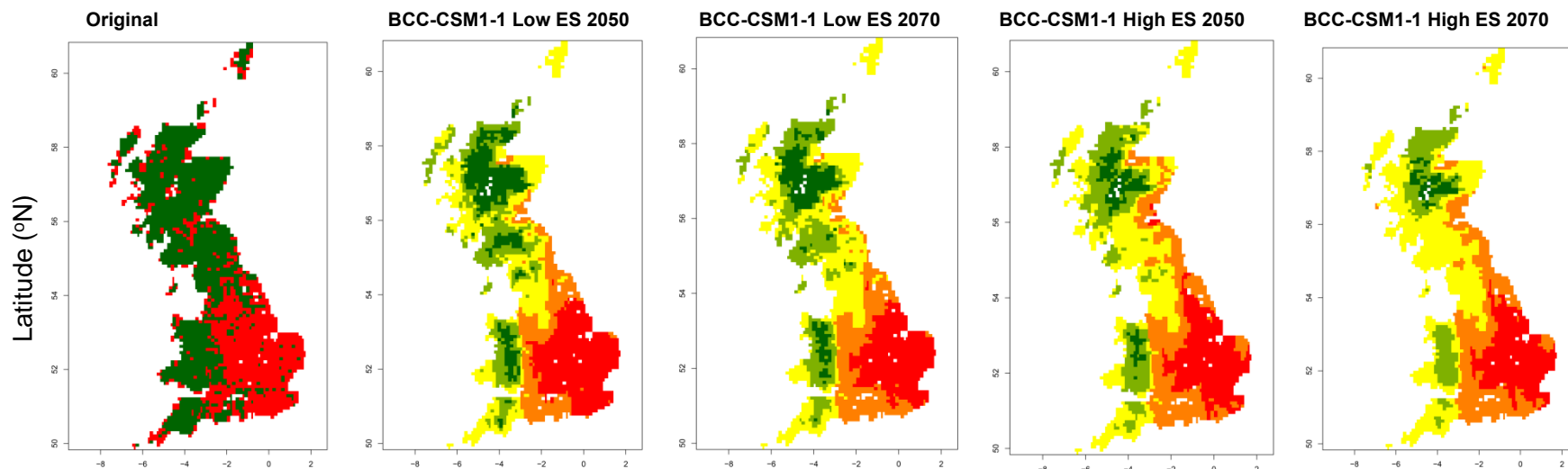
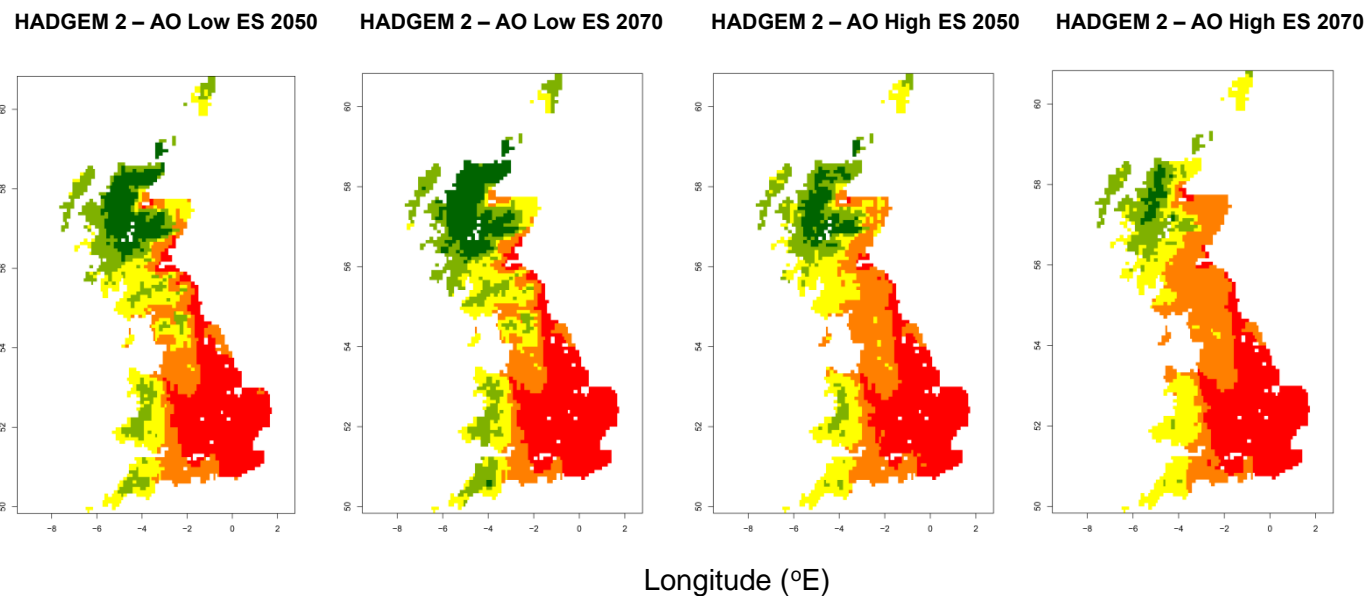
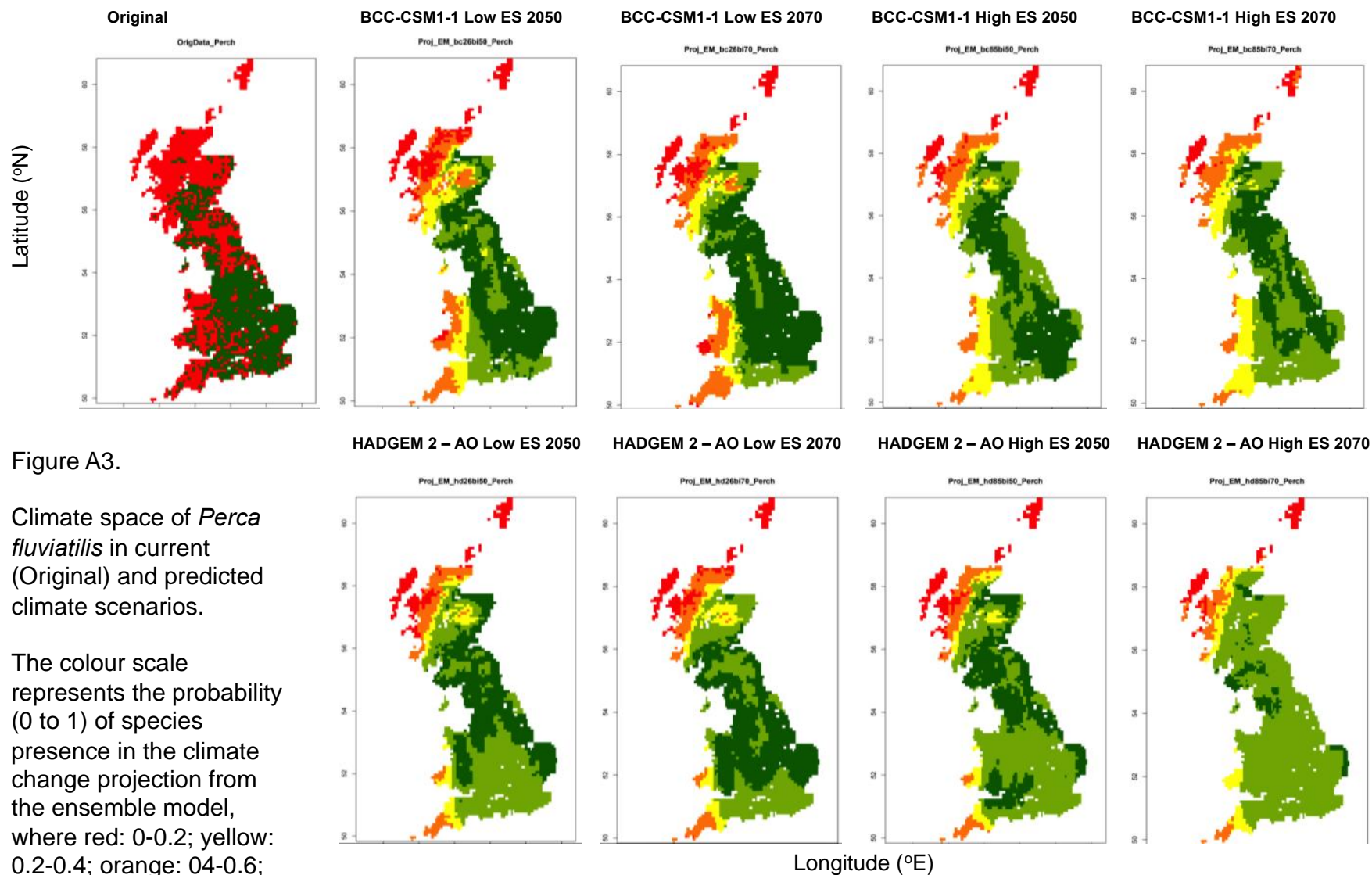


Figure A2.

Climate space of *Salmo salar* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0





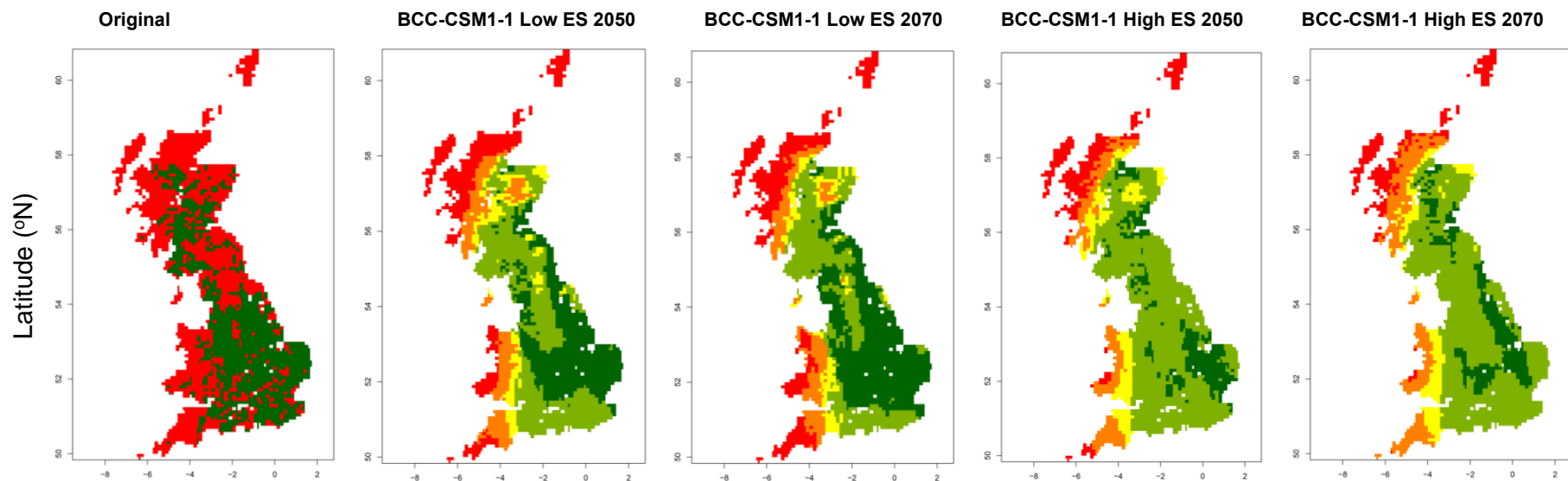
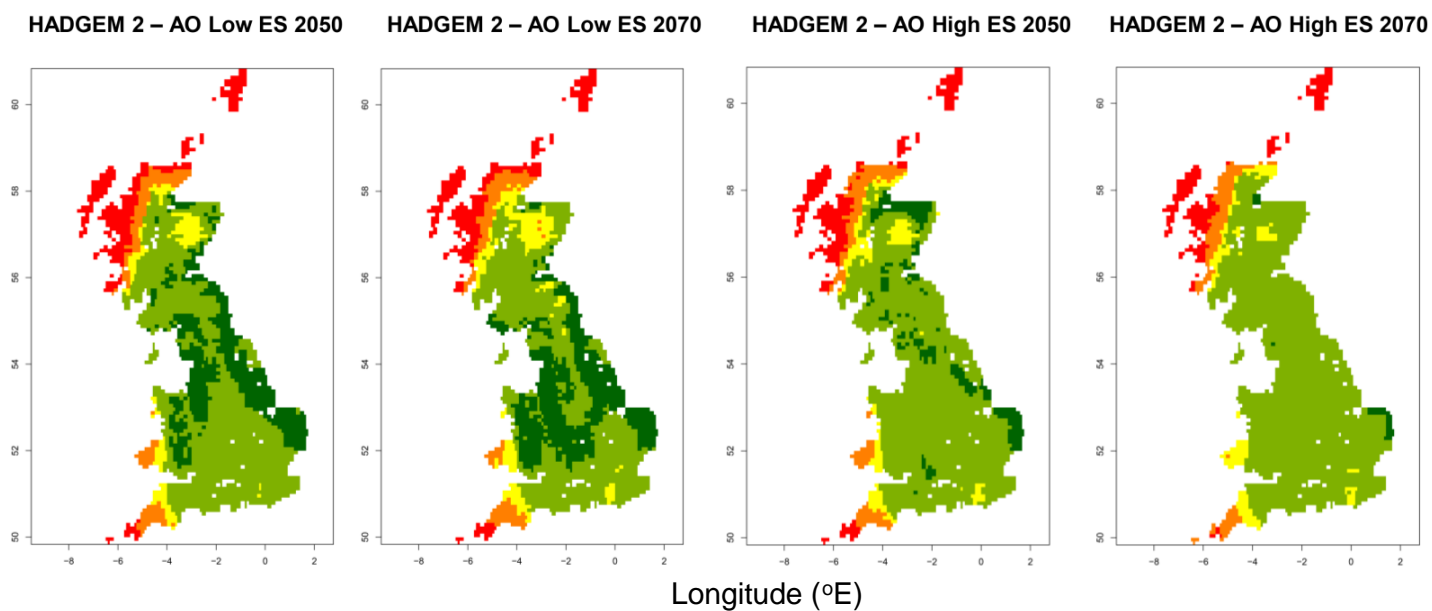


Figure A4.

Climate space of *Esox lucius* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0



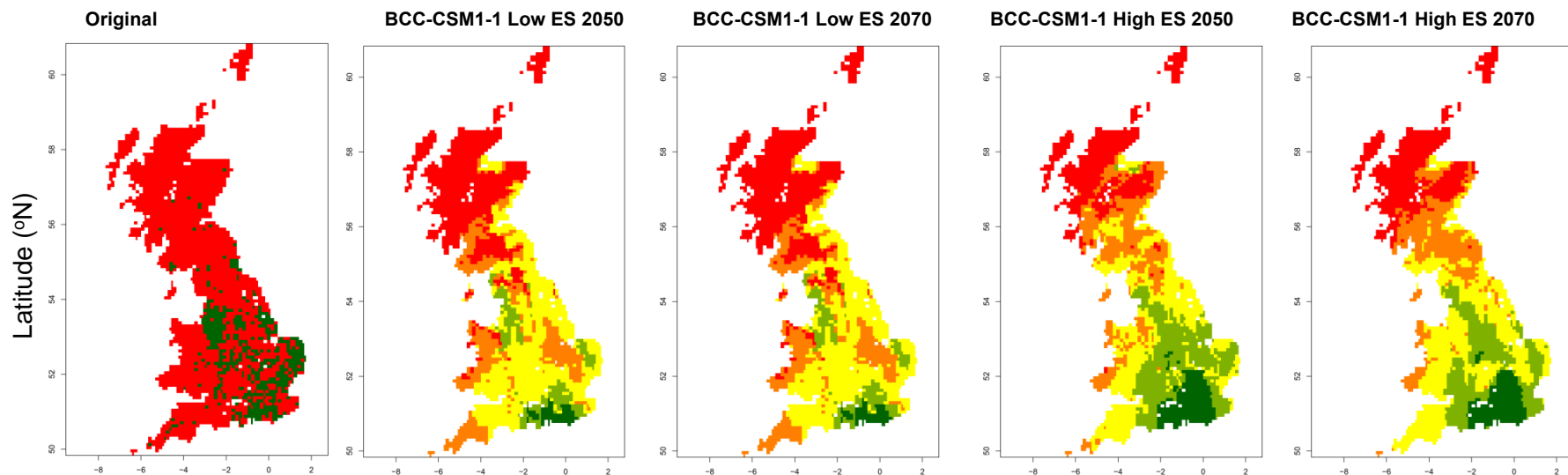
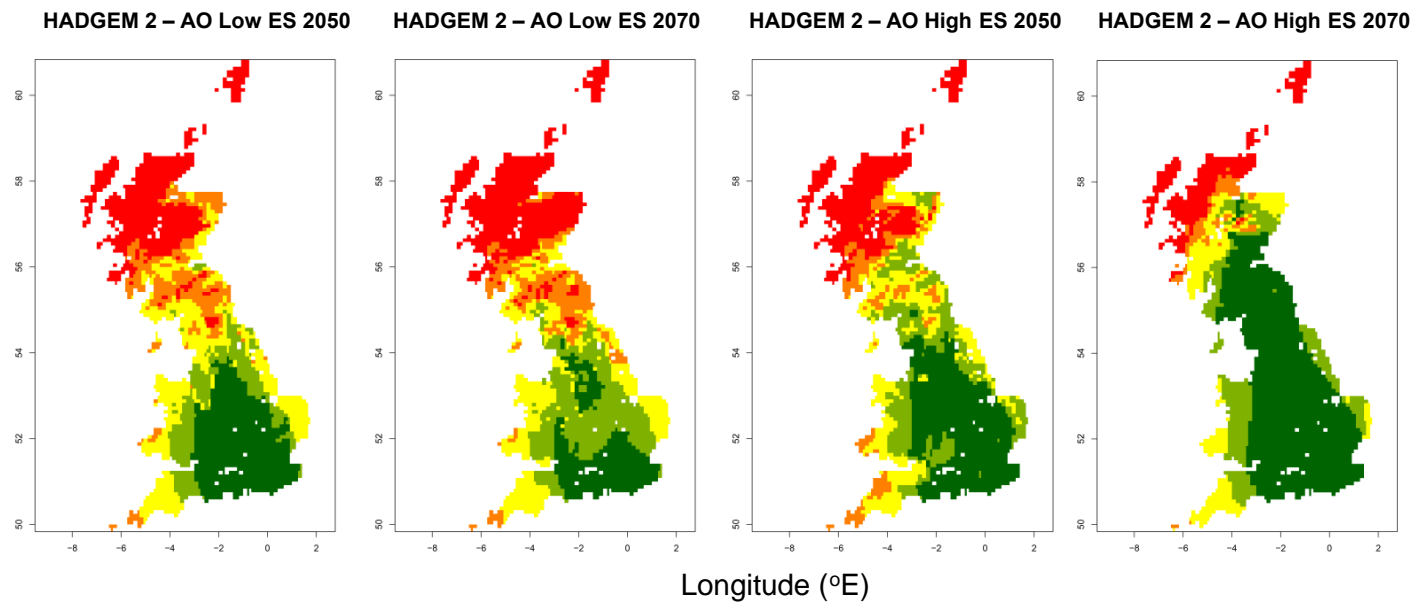


Figure A5.

Climate space of *Carassius carassius* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0



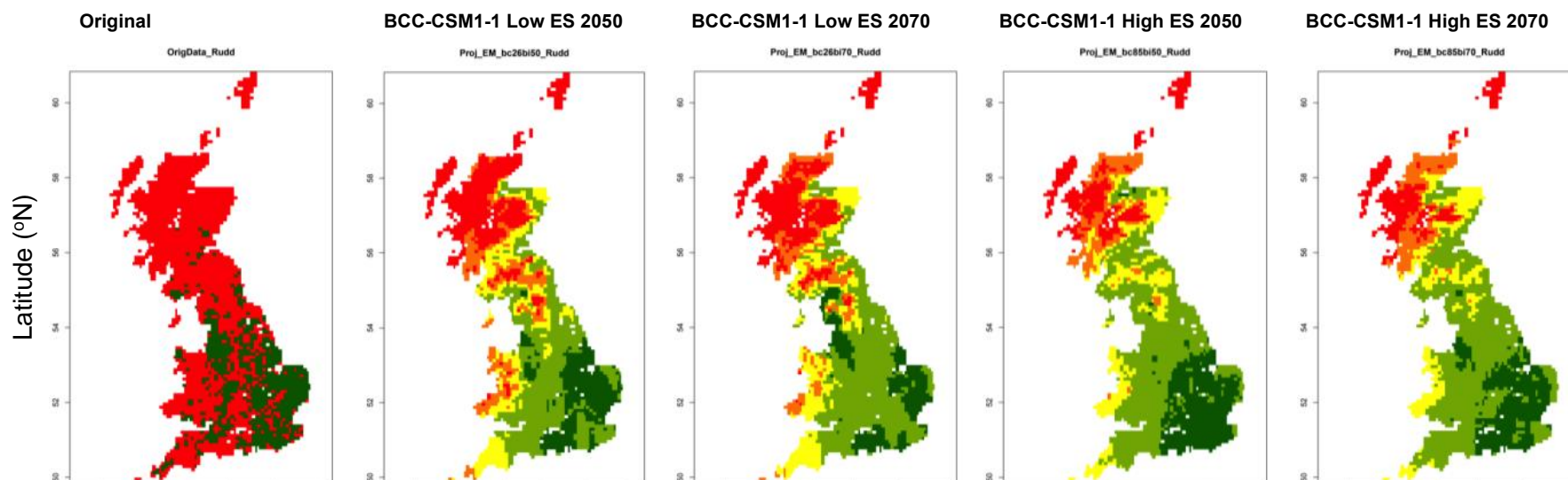
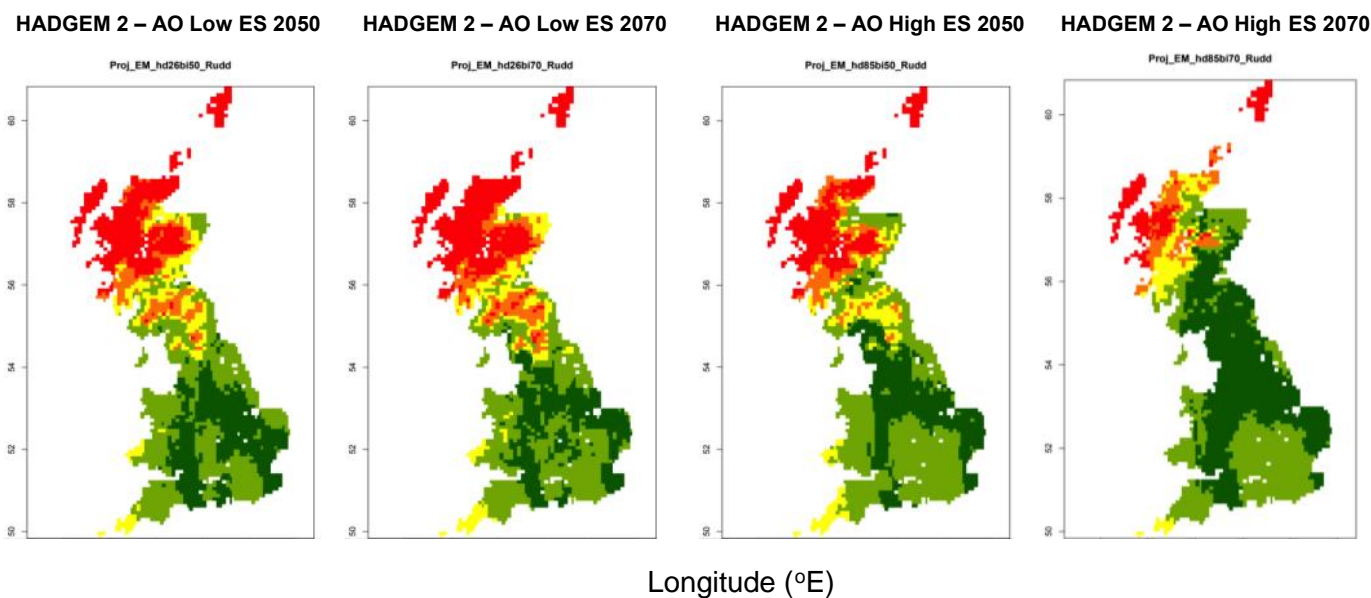


Figure A6.

Climate space of *Scardinius erythrophthalmus* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0



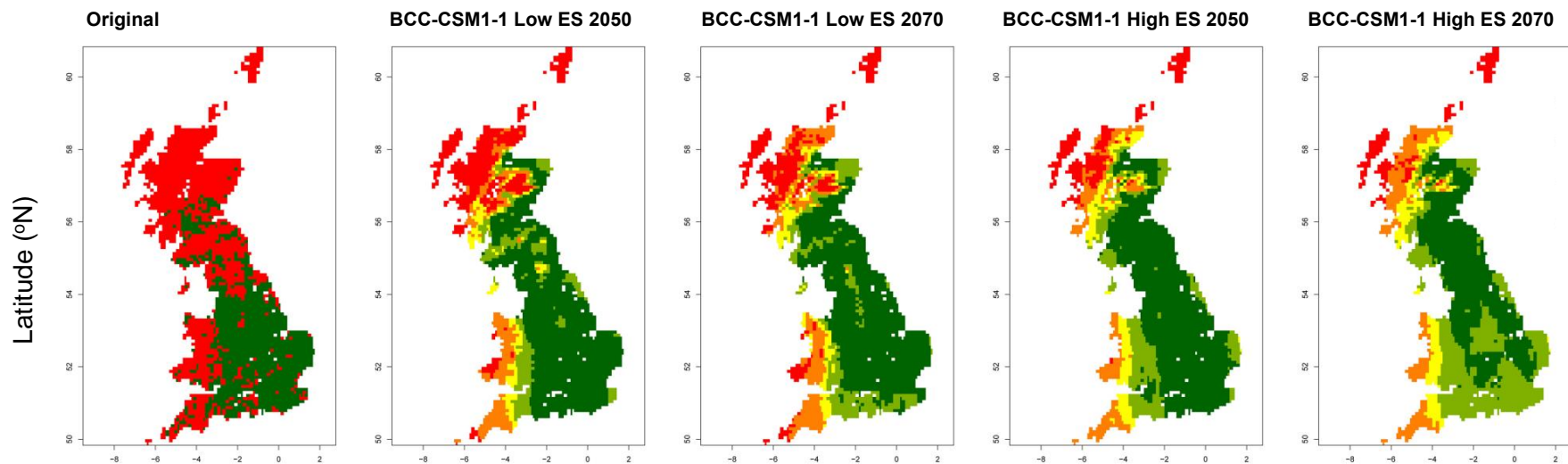
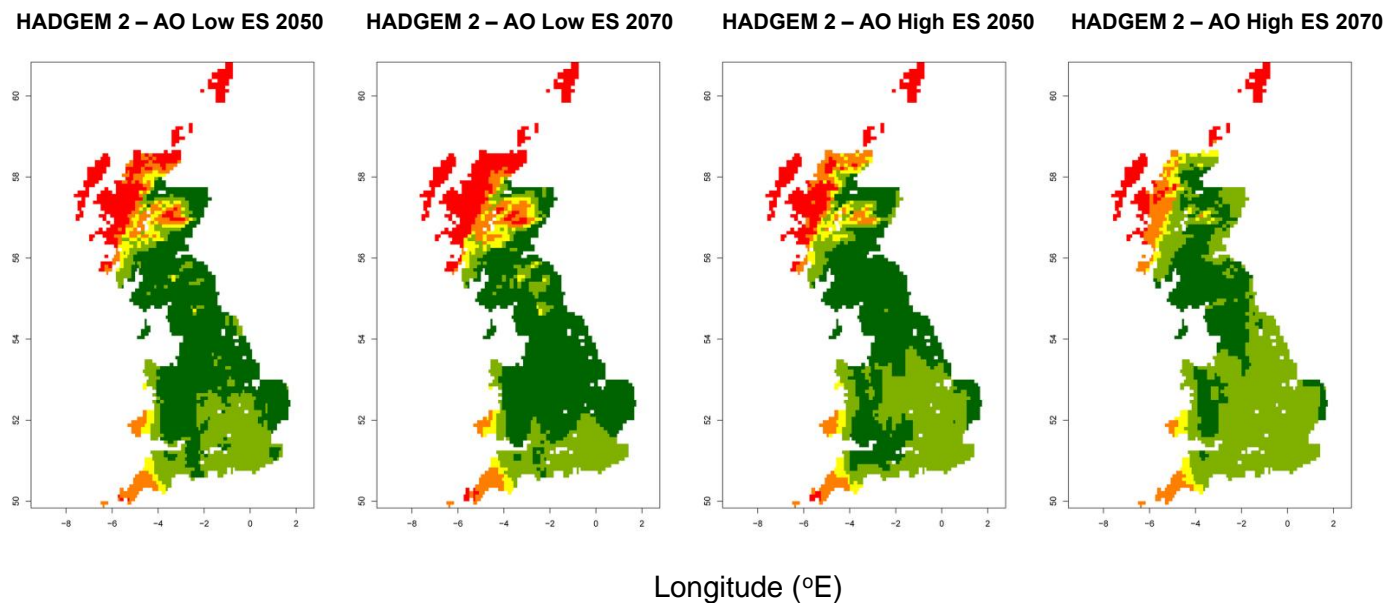


Figure A7.

Climate space of *Rutilus rutilus* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0



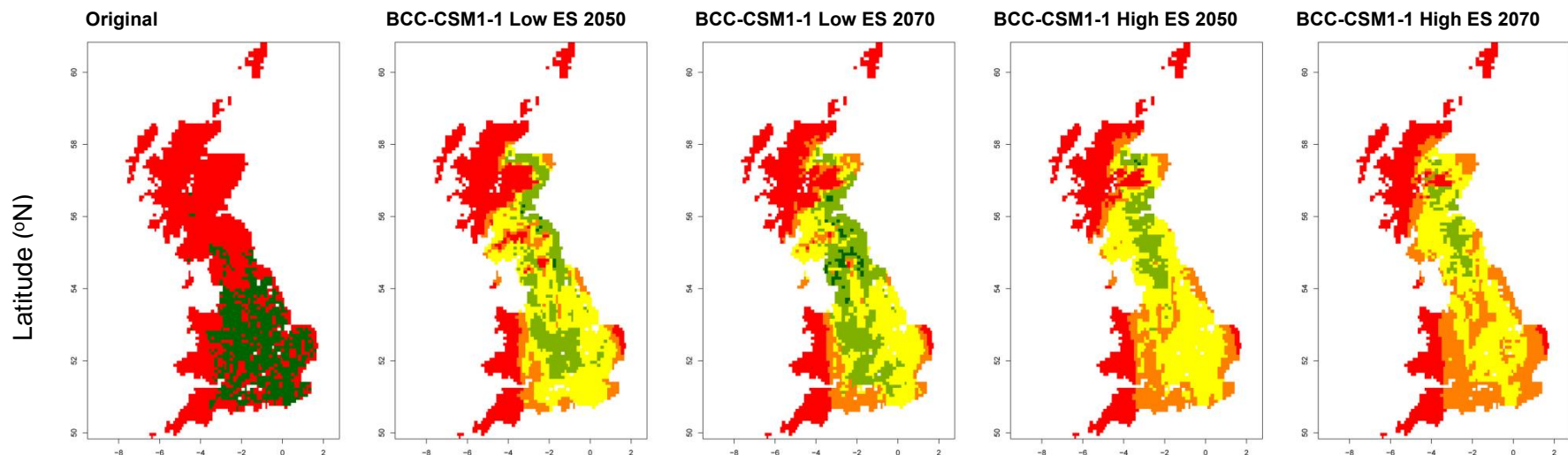
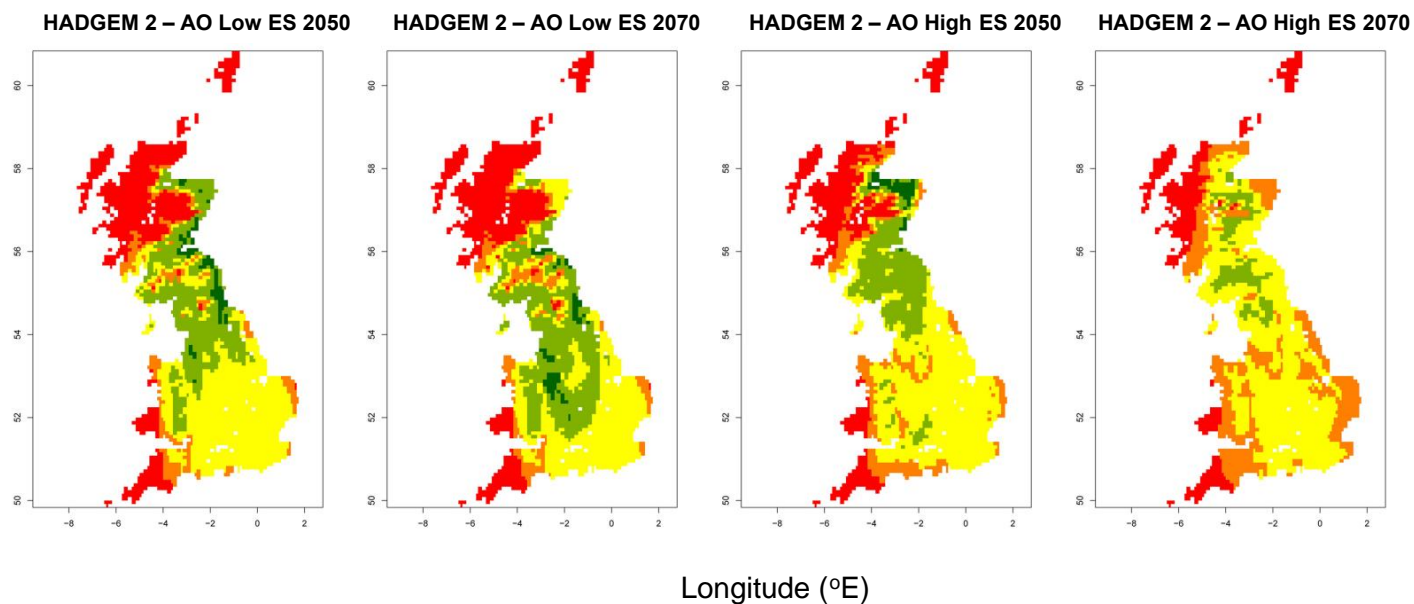


Figure A8.

Climate space of *Squalius cephalus* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0



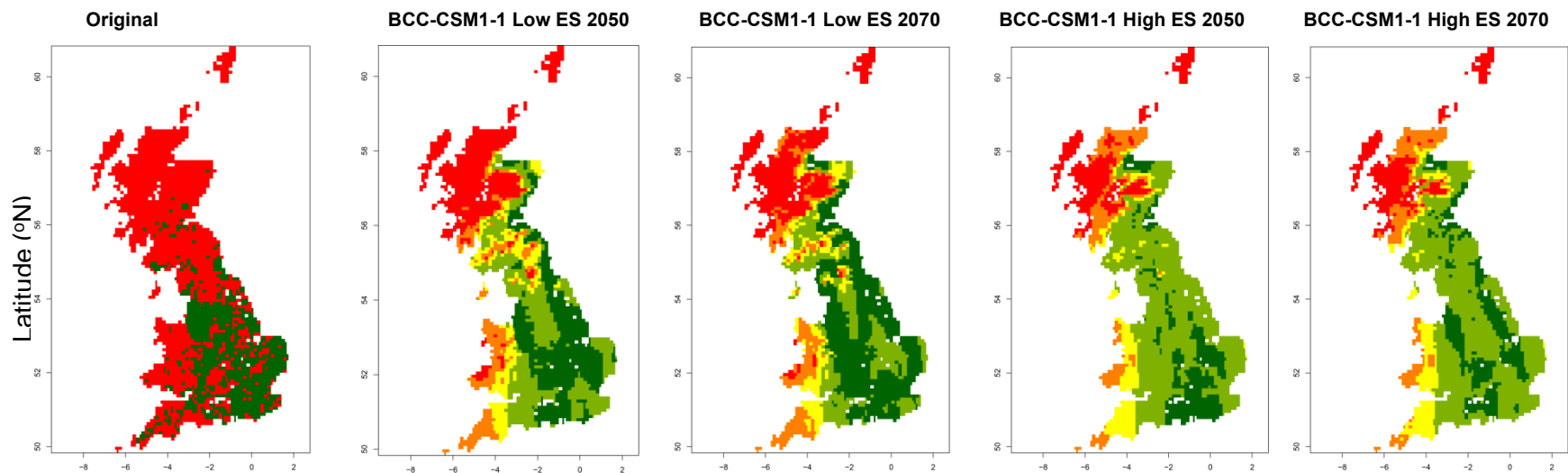
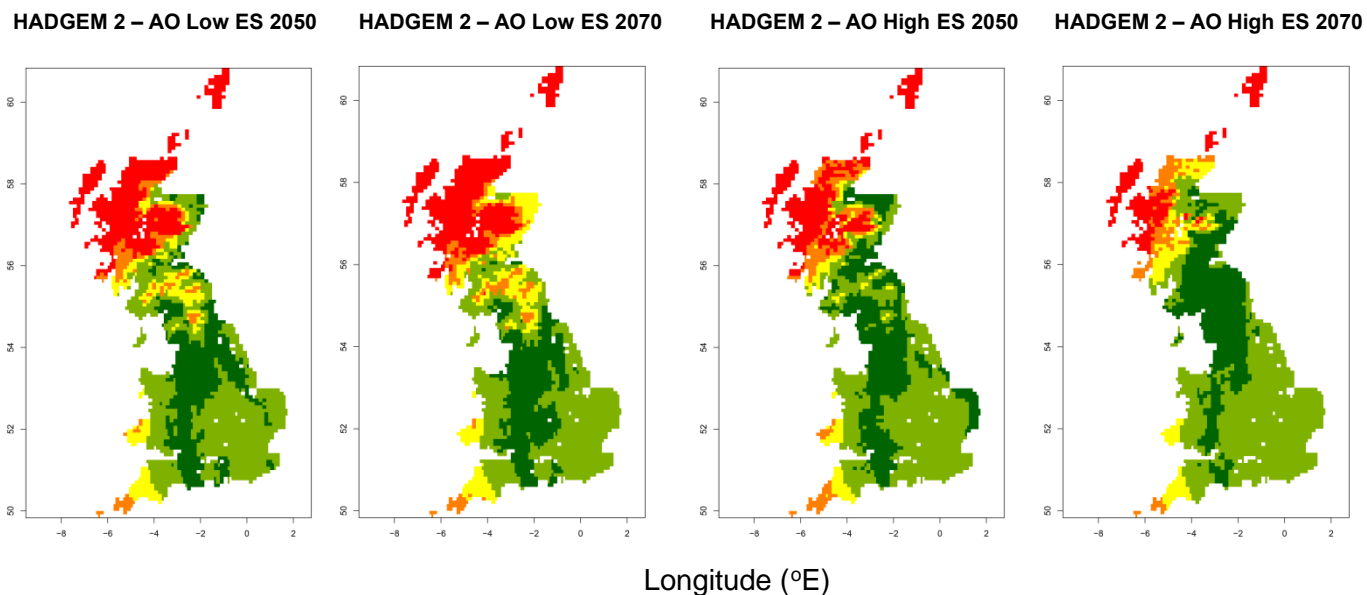


Figure A9.

Climate space of *Cyprinus carpio* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0



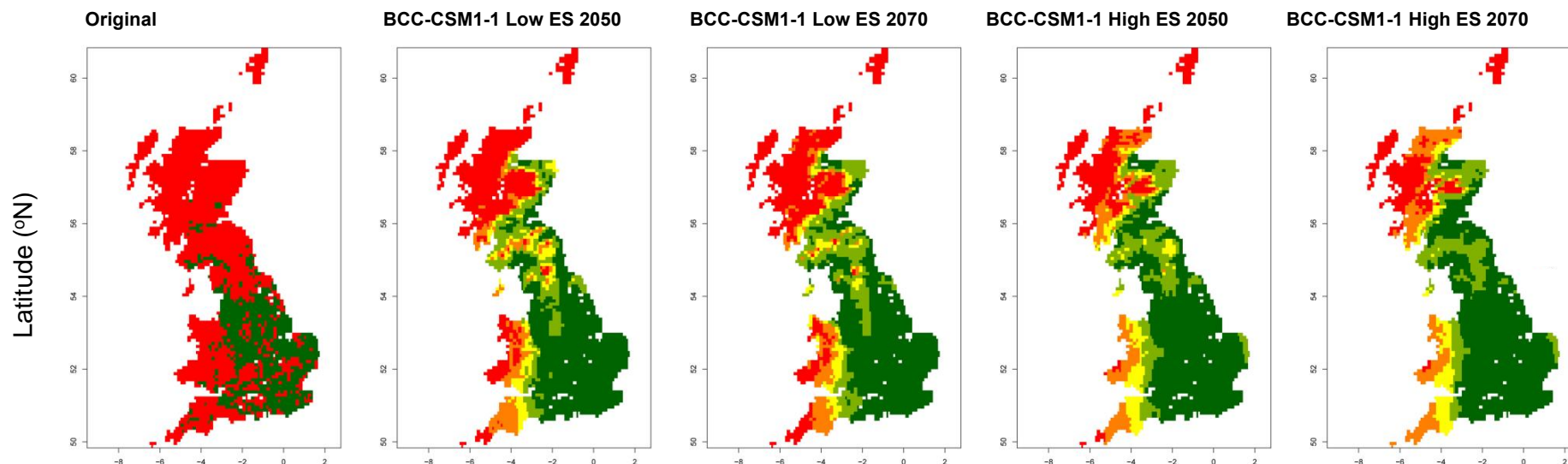
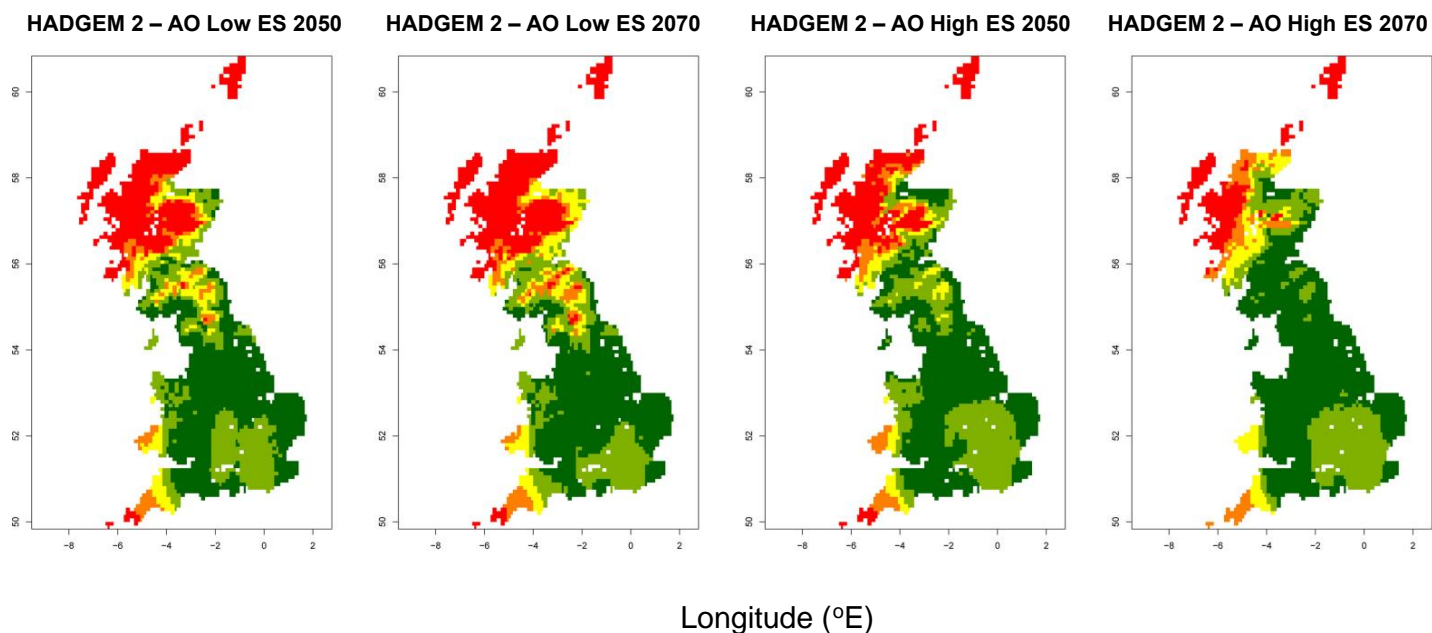


Figure A10.

Climate space of *Abramis brama* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0



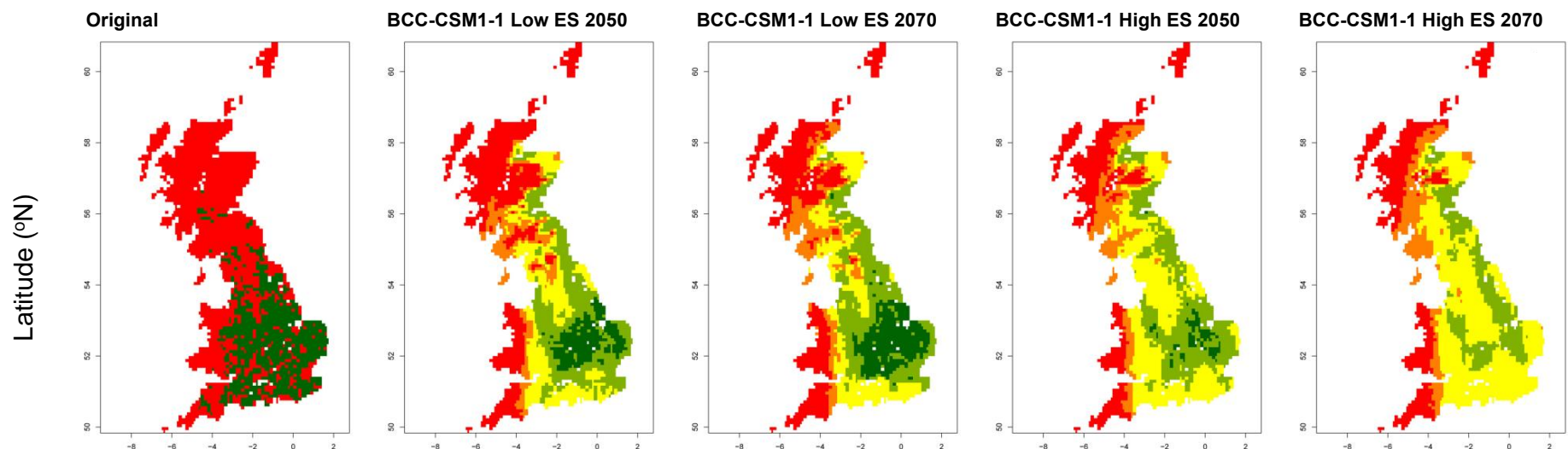
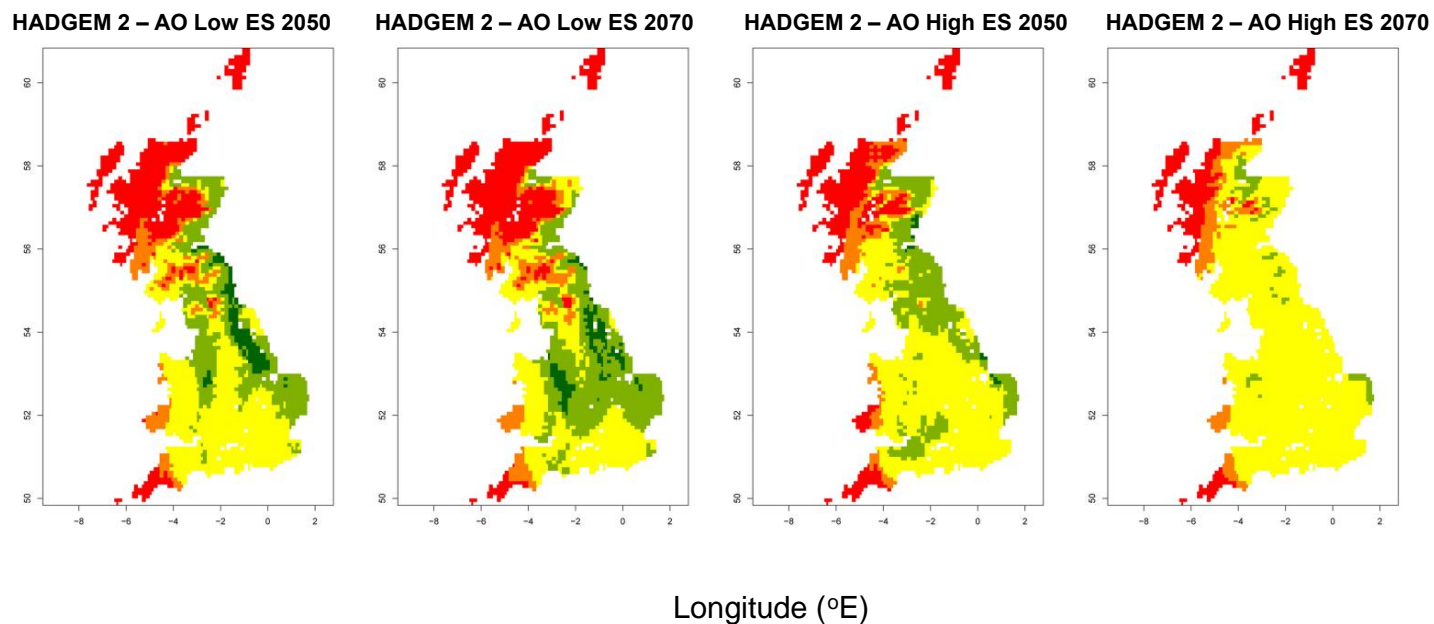


Figure A11.

Climate space of *Leuciscus leuciscus* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0



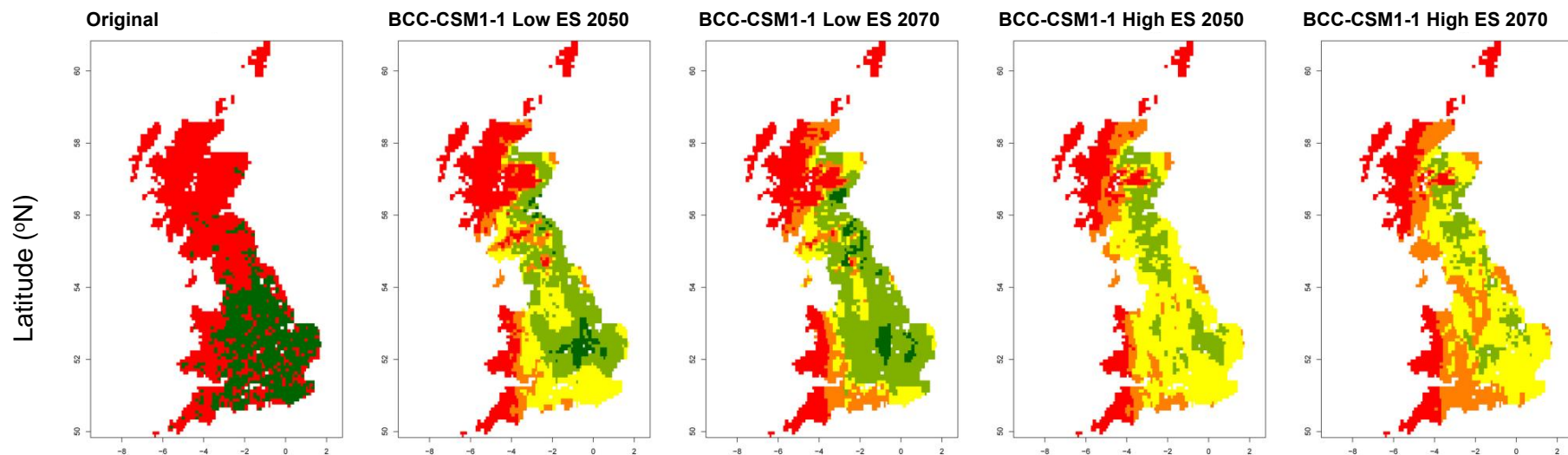


Figure A12.

Climate space of *Gobio gobio* in current (Original) and predicted climate scenarios.

The colour scale represents the probability (0 to 1) of species presence in the climate change projection from the ensemble model, where red: 0-0.2; yellow: 0.2-0.4; orange: 0.4-0.6; light green: 0.6-0.8; and dark green: 0.8-1.0

