UK National Ecosystems Assessment -Breeding Bird diversity as a function of Land Cover, Report to the Economics Team of the UK National Ecosystem Assessment

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Introduction

Birds are both the highest profile part of UK biodiversity with the general public and high in the food chain, so widely considered to be good indicators of wider ecosystem health. Birds are generally highly visible animals and thus provide a relatively easy form of wildlife for enthusiasts to view and record. Valuable, geographically sensitive, data is obtained from observers across the country which is not readily available for most other taxa in the UK. It has been demonstrated that birds can be sensitive to land use change, indeed, changes in farming practices have contributed to a 53% decrease in the England farmland bird index between 1966 and 2009 (DEFRA 2010). They are, therefore, the best available means by which to assess the biodiversity implications of land-use scenarios developed under the NEA.

The CEH Land Cover Map 2000 provides is source of data which can be very conveniently matched with existing data from the Breeding Bird Survey (BBS) collected by volunteers on behalf of the British Trust for Ornithology (BTO), Joint Nature Conservation Committee and Royal Society for the Protection of Birds. The BBS has been running in its current form since 1994 and thus provides data spanning the 2000 snapshot comprising the Land Cover Map.

Methods

The BBS is a line-transect survey of a random sample of 1 km squares. Squares are chosen through stratified random sampling, with more squares in areas with more potential volunteers. Observers make two early-morning visits to their square between April and June, recording all birds encountered while walking two 1 km transects across their square. Birds are recorded in three distance categories, or as ‘in flight’. The aim is for each volunteer to survey the same square (or squares) every year (Risely et al. 2010). For this analysis, in order to ensure adequate sample sizes, results of the surveys for the years 1995 – 2006 were used, which incorporates the year 2000, the year in which the land cover survey was conducted, and five years’ data on either side (there are no data available for 2001 due access restrictions arising from the foot-and-mouth outbreak). Records of birds in flight were discarded, as these individuals may not have been using the habitat within the square. Squares with data from only one year within the time period were discarded, as were records of bird species which were recorded on a mean of less than 40 squares per year. For each species, the maximum count across both visits in a year was extracted. Gull species were excluded because many records will have consisted of aggregations away from breeding sites. Counts for six wader species (Oystercatcher, Golden Plover, Lapwing, Snipe, Curlew and Redshank) were corrected to exclude counts from non-breeding flocks, and observations of Golden Plover in unsuitable breeding habitat are also excluded. The composition of the bird community represented by the presence and abundance of all remaining bird species in each survey square was summarized using Simpson’s Diversity Index (D), calculated in each year following Equation 1.

$$D = \frac{1}{\sum_{i=1}^{S} p_i^2} \qquad \text{Equation 1}$$

Where S = number of bird species recorded at a focal site in that year, p_i = proportion of birds of species i relative to the total number of birds of all species.

The mean value of D was calculated for each square across all years within the study period in which that square was surveyed and this became the dependent variable in the models. For each 1 km BBS grid square, the CEH Land Cover Map 2000 was used to derive the variables listed in Table 1. The habitats were based on the aggregate classes for the Land Cover Map, the broad habitat types listed in the NEA progress report of 18th October 2010 and expert knowledge of bird habitat preferences. The variables in Table 1 were then the sum of the percentage cover values for all subclasses in the square. Seven variables showed a curvilinear relationship with D when examined graphically as single variables, so a squared term was included where each occurred in the models to form quadratic functions; the exceptions were coastal habitat and inland water. The "mountain, heath and bog" category was correlated with the altitude at the centre of each 10km square (Pearson's r = 0.59, P<0.001) so altitude, which is often correlated with diversity, was left out of the model. This means that relationships with "mountain, heath and bog" could, instead, reflect effects of altitude that are unrelated to, but indistinguishable from, those of this habitat. In Great Britain, there are differences in the composition of bird communities with both latitude and longitude which do not always relate to the presence or absence of a particular habitat (at least to the extent that such habitats are distinguishable using Land Cover Map categories). The nuthatch, for example, has a northern limit to its distribution which does not match the availability of deciduous woodland, which is its preferred habitat within its range, although it is expanding northwards (Baillie et al 2010) and species such as redstart and wood warbler are more numerous in western deciduous woodland than in eastern deciduous woodland. To avoid the spurious relationships with particular habitat categories that such spatial patterns might produce, the 100km Ordnance Survey grid square in which each BBS square is located was included in the model as a factor.

General Linear Models were run using the GENMOD procedure in SAS 9.2 (SAS Institute 2000) with 100km square identity included in every model and using each of the 511 possible combinations of the nine land cover variables, squared terms were always fitted with the corresponding linear term. In order to account for variable survey effort across the UK and to ensure that the model results were equally applicable to all parts of the UK, a weighting variable was included in every model. The country was divided into the standard regions used in the organization of the BBS (N=80), the total number of BBS squares surveyed during each year being divided by the number of squares surveyed in that region during the same year. The weight value for each square used in the models was the mean weight value across the years in which that square was surveyed. The AIC value was calculated for each model, with the lowest value across models showing the best fit to the data. AIC weights were calculated for each variable and model-averaged parameter estimates calculated for each variable, squared term, level of the 100km factor and intercept along with model averaged standard errors, as per Burnham and Anderson (2002, 2004).

The model-averaged parameter estimates were used to calculate predicted diversity values for each $1km^2$ in the UK based on CEH 2000 land cover values and for each of the twelve NEA land-use change scenarios. The difference between these values was calculated to determine whether avian diversity was predicted to rise, fall or remain constant in each square. These predictions were illustrated spatially using maps of the change in bird diversity predicted for each scenario. Summary statistics are presented for the full set of twelve scenarios.

Results

A total of 3468 BBS squares across Great Britain were visited more than once between 1995 and 2006, and 96 bird species were recorded in a mean of 40 or more squares per year (Table 2). The best model (with the lowest AIC value) contained all variables except for coastal and inland water cover.

Model averaged parameter estimates for the land cover variables, with model averaged standard errors, are presented in Table 3, with those for 100km square levels being shown in Table 4. All land cover variables except for mountains, heaths and bogs showed positive linear parameter estimates and negative squared terms, indicating an increase in diversity at lower percentage cover of the habitat type which levels off or decreases with greater cover. Mountains, heaths and bogs had a negative linear term with a positive squared term, indicating a decrease in diversity with increased cover but that this decrease levels off with high percentage cover. The coastal habitat cover had a negative influence and inland water cover had a positive influence, but with high SEs and low variable AIC weights, suggesting that they had little influence. The deviance value of the lowest AIC model (Deviance= 3704722.9) was very large and does not fit the χ^2 distribution with 3408 degrees of freedom ($P<0.001$), indicating that there was significant variation in the diversity index that was unexplained by the model and that the model-averaged parameter set is unlikely to provide a very sound basis for prediction. The difference in AIC values between the top model and the same model without the regional control variable was 148.5, with the top model having the lowest AIC value, indicating that controlling for spatial variation in this way very much improves the model.

Table 1 Independent variables derived from CEH Land Cover Map 2000

Variable	CEH Land Map Subclasses
Coastal	sea/estuary Littoral rock Littoral sediment Saltmarsh supra-littoral rock supra-littoral sediment
Inland water	water (inland)
Arable and horticulture	arable cereals arable horticulture arable non-rotational
Deciduous woodland	deciduous woodland
Coniferous woodland	coniferous woodland
Improved grassland	improved grassland
Semi-natural grassland	Neutral grass setaside grass Bracken calcareous grass acid grassland fen/marsh/swamp
Mountain, heath and bog	Bog dense dwarf shrub heath open dwarf shrub heath montane habitats inland bare ground
Built up areas and gardens	suburban/rural development continuous urban

Table 2 Bird species with a mean of over 40 squares with non-flight BBS registrations that were included in the diversity calculation.

Species	Scientific name	Annual mean number of squares present ± SE
Mute Swan	*Cygnus olor*	164.73 ± 11.93
Greylag Goose	*Anser anser*	69.91 ± 8.98
Canada Goose	*Branta canadensis*	235.73 ± 20.88
Shelduck	*Tadorna tadorna*	85 ± 3.55
Mallard	*Anas platyrhynchos*	803.55 ± 46.06
Tufted Duck	*Aythya fuligula*	120.64 ± 5.73
Willow/Red Grouse	*Lagopus lagopus*	99.36 ± 3.07
Red-legged Partridge	*Alectoris rufa*	438.82 ± 31.28
Grey Partridge	*Perdix perdix*	209.27 ± 11.55
Pheasant	*Phasianus colchicus*	1420.64 ± 88.73
Little Grebe	*Tachybaptus ruficollis*	55.82 ± 4.84
Great Crested Grebe	*Podiceps cristatus*	58.45 ± 3.13
Cormorant	*Phalacrocorax carbo*	53.18 ± 5.03
Grey Heron	*Ardea cinerea*	230.82 ± 15.73
Sparrowhawk	*Accipiter nisus*	94.00 ± 7.31
Buzzard	*Buteo buteo*	349.27 ± 38.75
Kestrel	*Falco tinnunculus*	312.36 ± 20.62
Moorhen	*Gallinula chloropus*	552.45 ± 27.49
Coot	*Fulica atra*	219.82 ± 14.19
Oystercatcher	*Haematopus ostralegus*	202.73 ± 8.21
Golden Plover	*Pluvialis apricaria*	49.73 ± 3.03
Lapwing	*Vanellus vanellus*	460.73 ± 19.56
Snipe	*Gallinago gallinago*	107.27 ± 3.72
Curlew	*Numenius arquata*	342.73 ± 7.45
Redshank	*Tringa tetanus*	62.27 ± 2.58
Common Sandpiper	*Actitis hypoleucos*	55.27 ± 3.24
Feral pigeon	*Columba livia*	383.82 ± 21.07
Stock Dove	*Columba oenas*	468.36 ± 24.31
Woodpigeon	*Columba palumbus*	1932.18 ± 95.07
Collared Dove	*Streptopelia decaocto*	1048.18 ± 61.02
Turtle Dove	*Streptopelia turtur*	161.00 ± 8.06
Cuckoo	*Cuculus canorus*	645.82 ± 26.35
Little Owl	*Athene noctua*	91.00 ± 4.42
Tawny Owl	*Strix aluco*	75.64 ± 4.32
Swift	*Apus apus*	111.73 ± 5.05
Green Woodpecker	*Picus viridis*	632.00 ± 49.02
Great Spotted Woodpecker	*Dendrocopos major*	724.55 ± 72.35
Skylark	*Alauda arvensis*	1364.91 ± 52.67
Swallow	*Hirundo rustica*	794.73 ± 44.05

Table 2 *cont*.

Species	Scientific name	Annual mean number of squares present ± SE
House Martin	*Delichon urbica*	278.27 ± 9.77
Tree Pipit	*Anthus trivialis*	118.64 ± 4.77
Meadow Pipit	*Anthus pratensis*	592.09 ± 20.38
Yellow Wagtail	*Motacilla flava*	133.00 ± 4.37
Grey Wagtail	*Motacilla cinerea*	149.73 ± 11.54
Pied Wagtail	*Motacilla alba*	959.18 ± 49.74
Dipper	*Cinclus cinclus*	42.82 ± 2.57
Wren	*Troglodytes troglodytes*	1958.27 ± 97.58
Dunnock	*Prunella modularis*	1646.64 ± 87.86
Robin	*Erithacus rubecula*	1893.64 ± 95.96
Redstart	*Phoenicurus phoenicurus*	138.82 ± 5.45
Whinchat	*Saxicola rubetra*	71.36 ± 4.03
Stonechat	*Saxicola torquata*	105.00 ± 14.77
Wheatear	*Oenanthe oenanthe*	249.82 ± 10.25
Blackbird	*Turdus merula*	1977.36 ± 98.16
Song Thrush	*Turdus philomelos*	1557.09 ± 92.07
Mistle Thrush	*Turdus viscivorus*	937.09 ± 42.66
Grasshopper Warbler	*Locustella naevia*	48.73 ± 3.39
Sedge Warbler	*Acrocephalus schoenobaenus*	231.64 ± 8.3
Reed Warbler	*Acrocephalus scirpaceus*	102.82 ± 7.28
Blackcap	*Sylvia atricapilla*	1226.64 ± 87.26
Garden Warbler	*Sylvia borin*	392.55 ± 16.87
Lesser Whitethroat	*Sylvia curruca*	222.82 ± 13.1
Whitethroat	*Sylvia communis*	1108.64 ± 59.21
Wood Warbler	*Phylloscopus sibilatrix*	51.45 ± 3.15
Chiffchaff	*Phylloscopus collybita*	1113.18 ± 77.18
Willow Warbler	*Phylloscopus trochilus*	1173.82 ± 37.92
Goldcrest	*Regulus regulus*	612.82 ± 45.4
Spotted Flycatcher	*Muscicapa striata*	184.91 ± 7.39
Pied Flycatcher	*Ficedula hypoleuca*	40.27 ± 2
Long-tailed Tit	*Aegithalos caudatus*	707.82 ± 46.67
Blue Tit	*Cyanistes caeruleus*	1857.55 ± 95.06
Great Tit	*Parus major*	1729.18 ± 101.17
Coal Tit	*Parus ater*	588.00 ± 35.84
Willow Tit	*Parus montanus*	51.00 ± 3.22
Marsh Tit	*Parus palustris*	130.82 ± 5.23
Nuthatch	*Sitta europaea*	364.00 ± 31.04
Treecreeper	*Certhia familiaris*	285.27 ± 13.58
Jay	*Garrulus glandarius*	516.82 ± 34.65
Magpie	*Pica pica*	1442.55 ± 71.46
Jackdaw	*Corvus monedula*	1113.64 ± 68.64
Rook	*Corvus frugilegus*	812.91 ± 29.77
Carrion Crow	*Corvus corone*	1791.73 ± 94.78
Raven	*Corvus corax*	80.55 ± 7.83

Table 2 *cont.*

Species	Scientific name	Annual mean number of squares present ± SE
Starling	*Sturnus vulgaris*	1364.18 ± 44.96
House Sparrow	*Passer domesticus*	1323.55 ± 57.17
Tree Sparrow	*Passer montanus*	134.73 ± 5.2
Chaffinch	*Fringilla coelebs*	1979.73 ± 98.1
Greenfinch	*Carduelis chloris*	1454.09 ± 92.87
Goldfinch	*Carduelis carduelis*	1045.00 ± 71.58
Siskin	*Carduelis spinus*	91.55 ± 4.5
Linnet	*Carduelis cannabina*	922.91 ± 26.37
Lesser Redpoll	*Carduelis cabaret*	71.55 ± 4.11
Bullfinch	*Pyrrhula pyrrhula*	453.82 ± 26.71
Yellowhammer	*Emberiza citrinella*	1038.18 ± 32.03
Reed Bunting	*Emberiza schoeniclus*	357.64 ± 24.75
Corn Bunting	*Miliaria calandra*	132.73 ± 6.53

Table 3 Model-averaged parameter estimates, their standard errors and AIC weights for land cover variables.

Variable	Model averaged parameter estimate ± SE	Variable AIC weight
Intercept	2.29306 ± 3.62556	NA
Arable	0.02844 ± 0.01567	0.80
Arable^2	-0.00016 ± 0.00011	
Deciduous woodland	0.15126 ± 0.01755	1.00
Deciduous woodland^2	-0.00188 ± 0.00026	
Coniferous woodland	0.06773 ± 0.01639	1.00
Coniferous woodland^2	-0.00094 ± 0.00013	
Improved grassland	0.05034 ± 0.01437	1.00
Improved grassland^2	-0.00038 ± 0.00012	
Unimproved grassland	0.0167 ± 0.01521	1.00
Unimproved grassland^2	-0.00063 ± 0.0001	
Urban	0.06978 ± 0.01706	1.00
Urban^2	-0.00126 ± 0.00014	
Mountains, heaths and bogs	-0.08134 ± 0.0118	1.00
Mountains, heaths and bogs^2	0.00024 ± 0.00011	
Coastal habitat	-0.01183 ± 0.01505	0.58
Inland water	0.01265 ± 0.02121	0.53

Table 4. Model-averaged estimates for levels of 100km square class.

Ordnance Survey 100km Square	Model averaged parameter estimate ± SE
HU	6.22 ± 3.46
HY	1.74 ± 3.52
NB	5.49 ± 3.42
NC	6.22 ± 3.40
ND	5.93 ± 3.45
NF	5.49 ± 3.44
NG	5.78 ± 3.41
NH	6.43 ± 3.40
NJ	4.83 ± 3.40
NK	6.28 ± 3.75
NL	3.31 ± 3.69
NM	6.01 ± 3.41
NN	5.60 ± 3.40
NO	5.52 ± 3.40
NR	6.52 ± 3.42
NS	6.05 ± 3.40
NT	5.37 ± 3.40
NU	6.64 ± 3.48
NX	7.00 ± 3.40
NY	6.15 ± 3.40
NZ	7.60 ± 3.41
SD	7.46 ± 3.40
SE	7.04 ± 3.40
SH	7.72 ± 3.40
SJ	8.03 ± 3.40
SK	7.82 ± 3.40
SM	7.43 ± 3.47
SN	8.25 ± 3.40
SO	7.95 ± 3.40
SP	6.99 ± 3.40
SR	9.18 ± 4.55
SS	7.16 ± 3.42
ST	7.40 ± 3.40
SU	6.63 ± 3.40
SW	7.69 ± 3.44
SX	6.83 ± 3.41
SY	6.96 ± 3.45
SZ	6.35 ± 3.50
TA	7.51 ± 3.42
TF	6.69 ± 3.41
TG	7.00 ± 3.45
TL	7.76 ± 3.40
TM	6.75 ± 3.42
TQ	7.08 ± 3.40
TR	7.07 ± 3.47
TV	0.00 ± 0.00

Scenario Results

For each scenario the predicted change in Simpson's Diversity index from the predictions based on the baseline CEH Land Cover 2000 data is displayed in Figure 1.

Fig. 1 a) GF Low

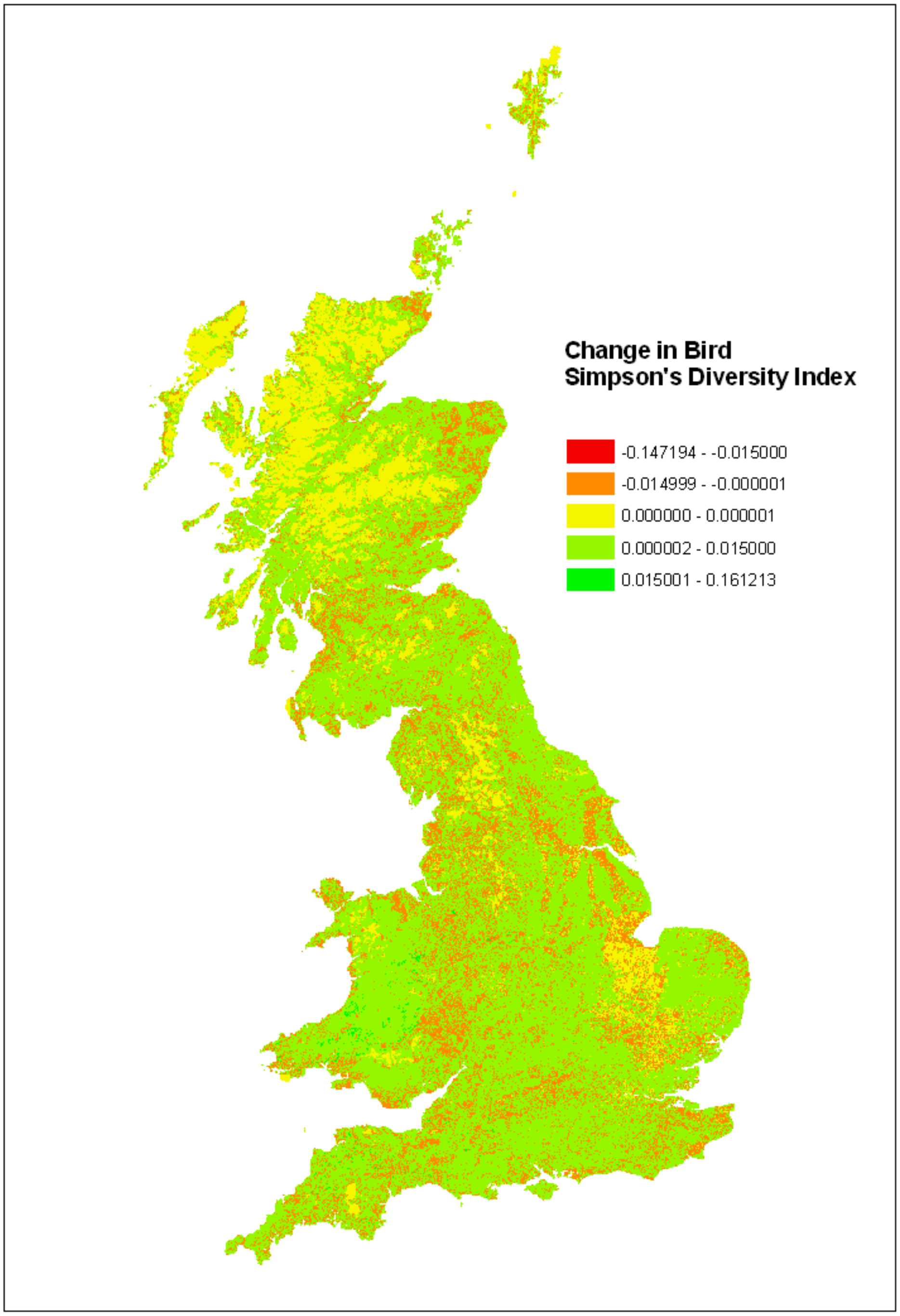

Fig. 1 b) GF High

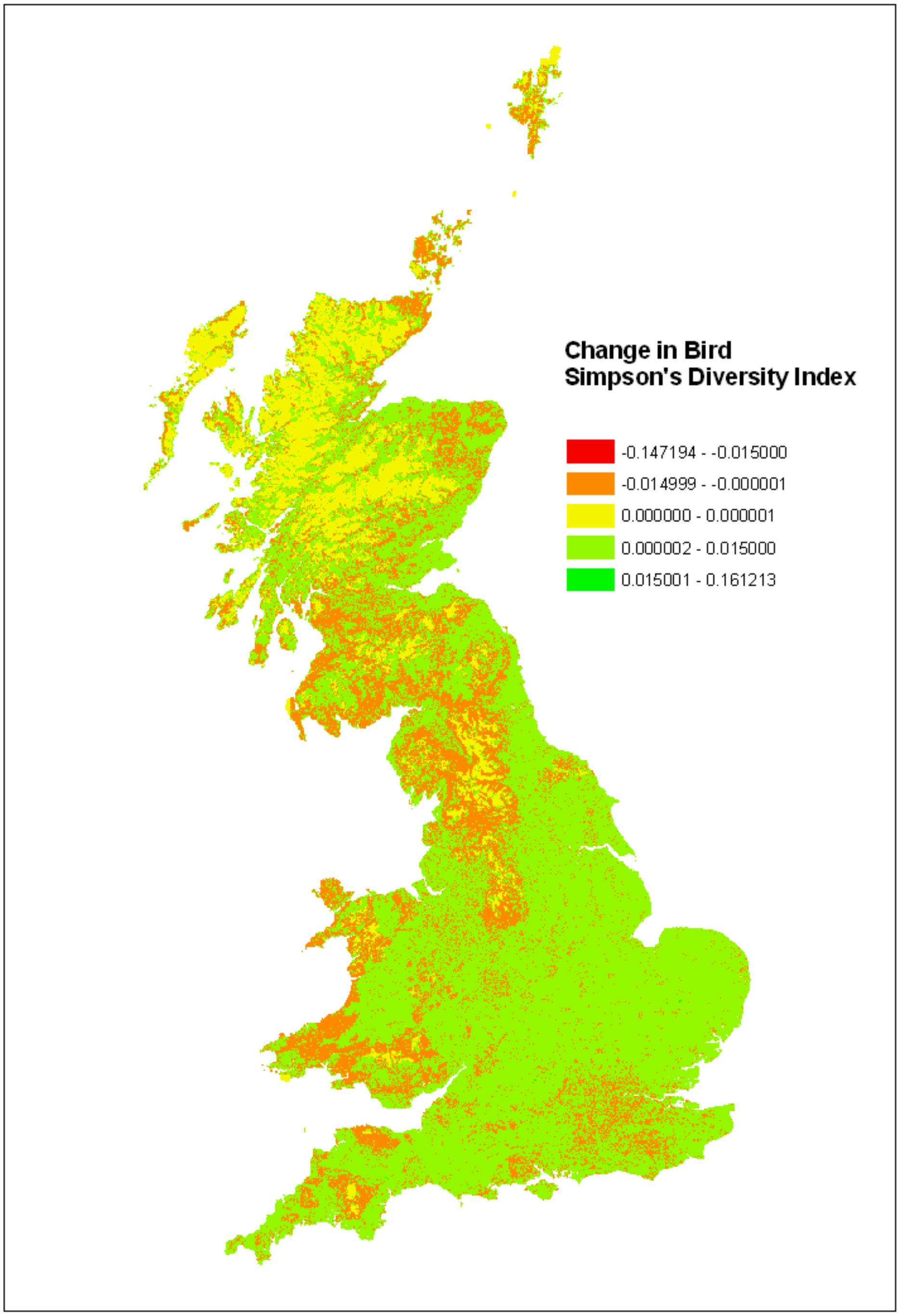

Fig. 1 c) GPL Low

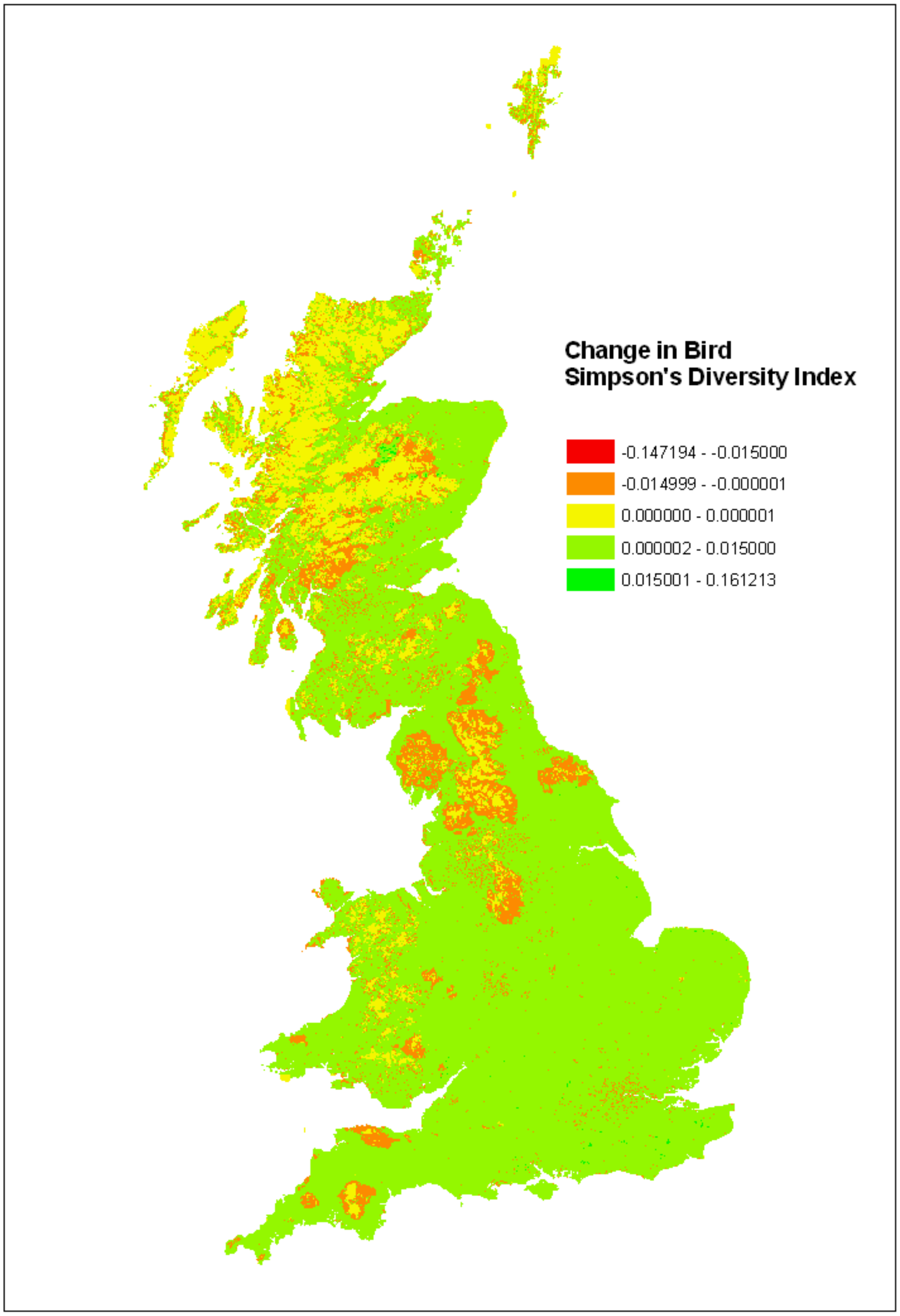

Fig. 1 d) GPL High

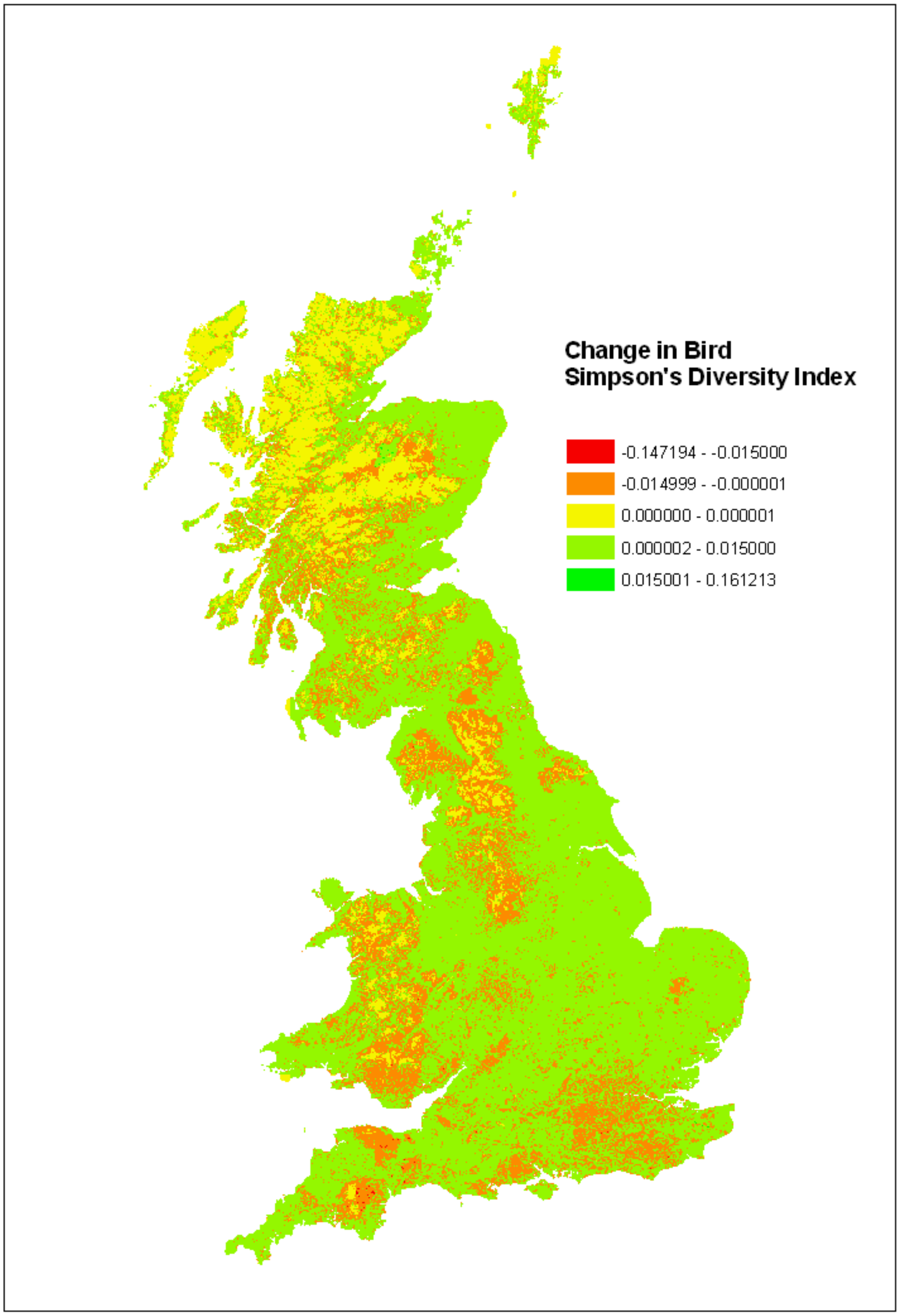

Fig. 1 e) LS Low

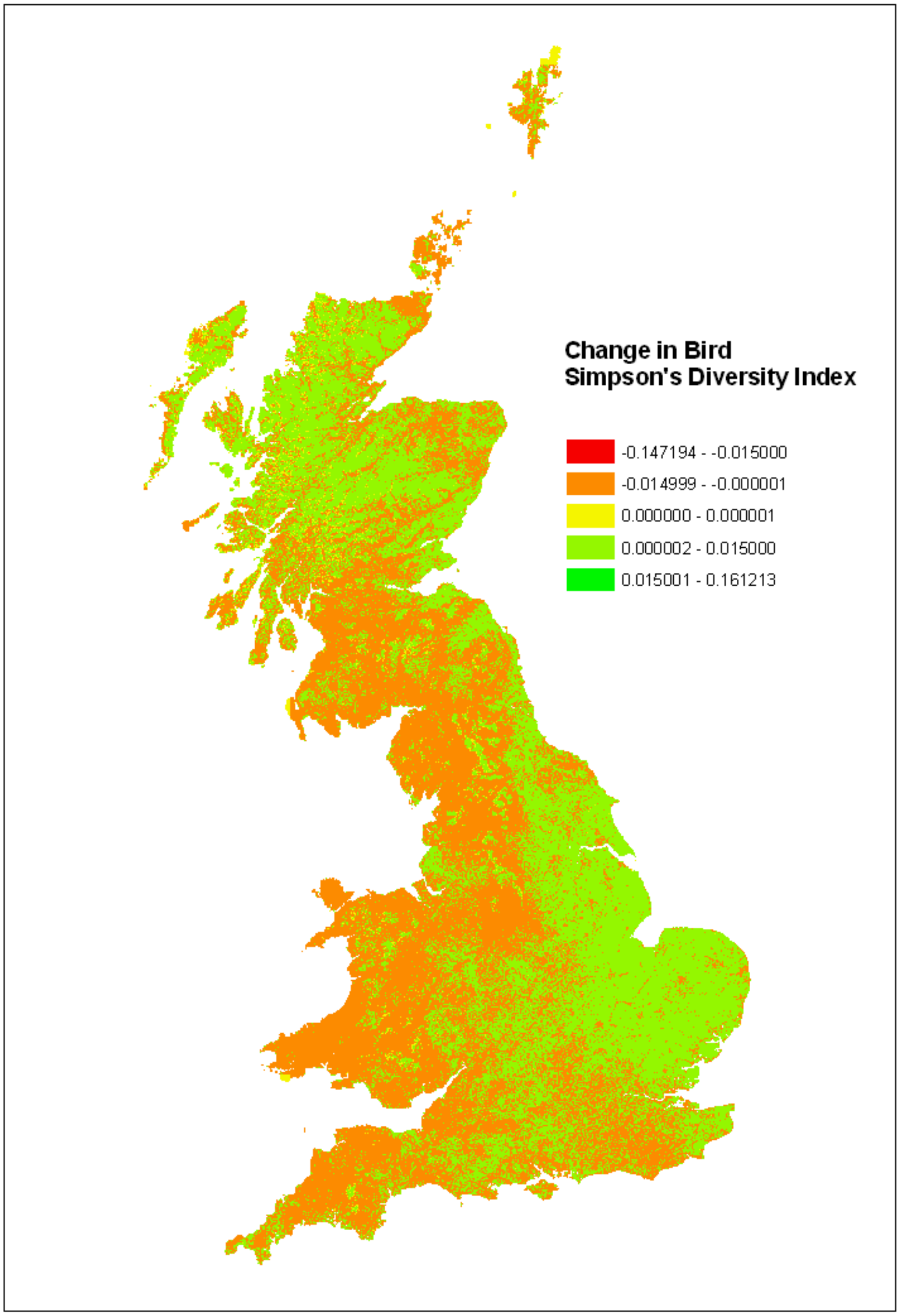
Change in Bird
Simpson's Diversity Index
-0.147194 - -0.015000
-0.014999 - -0.000001
0.000000 - 0.000001
0.000002 - 0.015000
0.015001 - 0.161213

Fig. 1 f) LS High

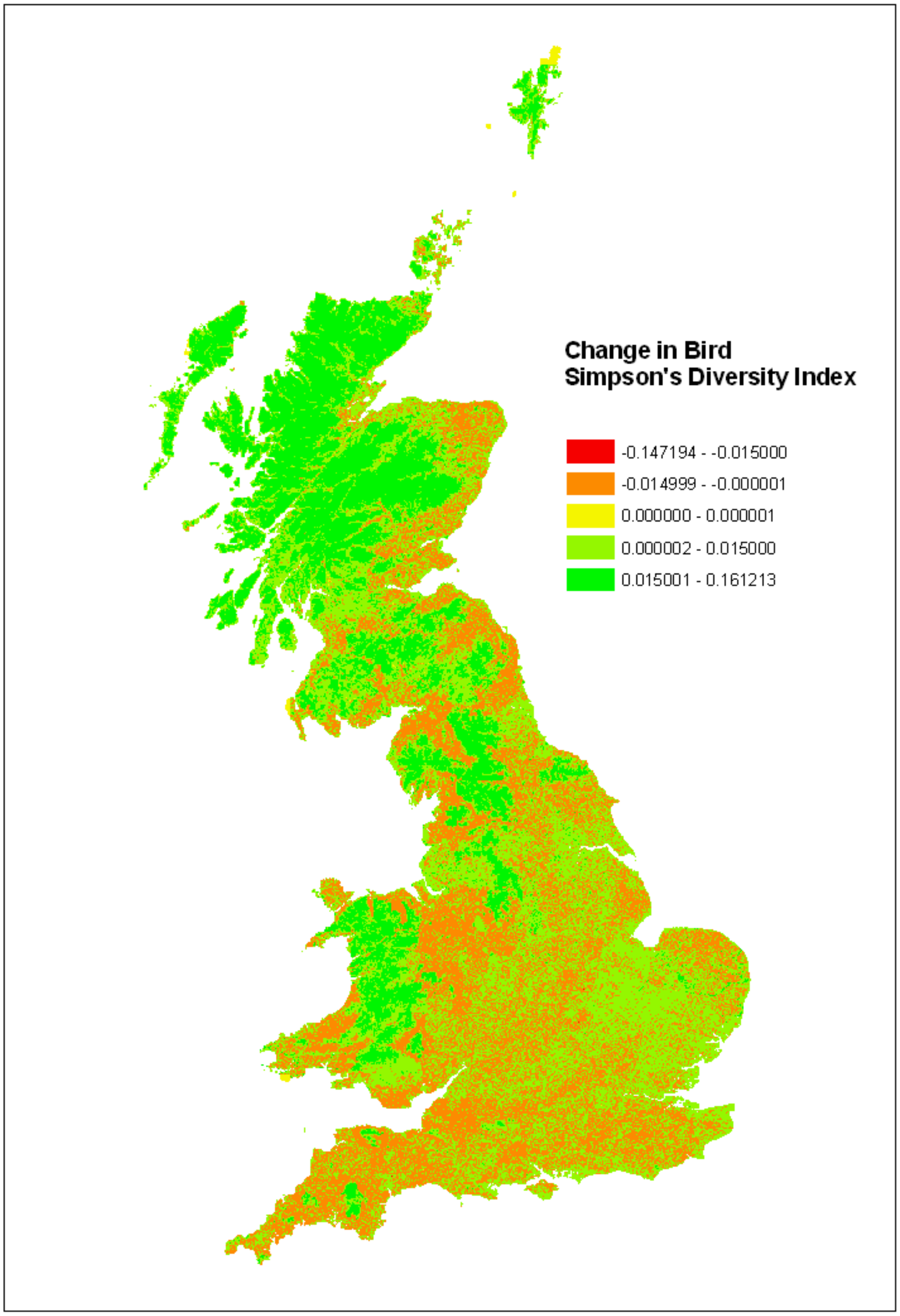

Fig. 1 g) NS Low

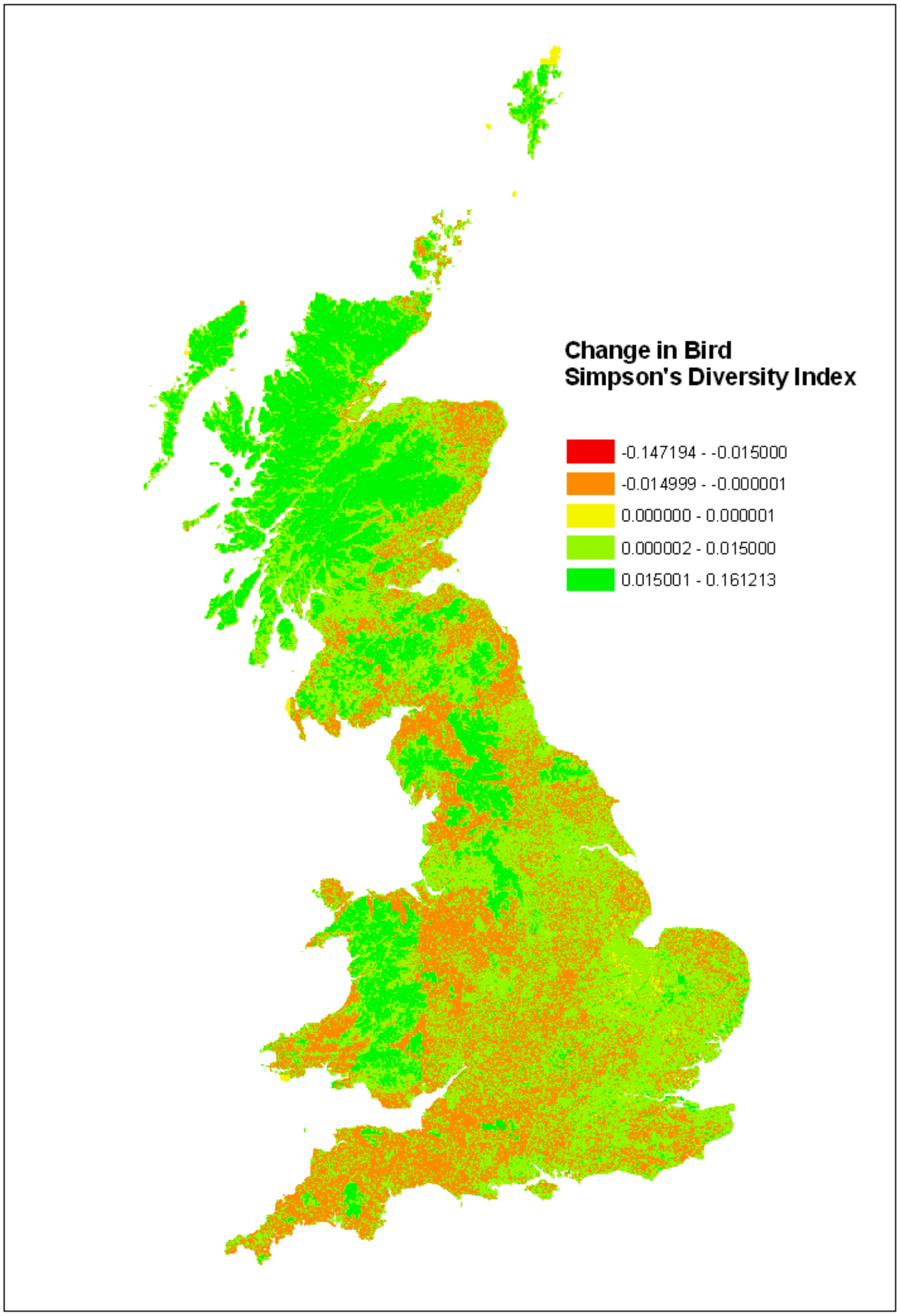
Change in Bird
Simpson's Diversity Index
-0.147194 - -0.015000
-0.014999 - -0.000001
0.000000 - 0.000001
0.000002 - 0.015000
0.015001 - 0.161213

Fig. 1 h) NS High

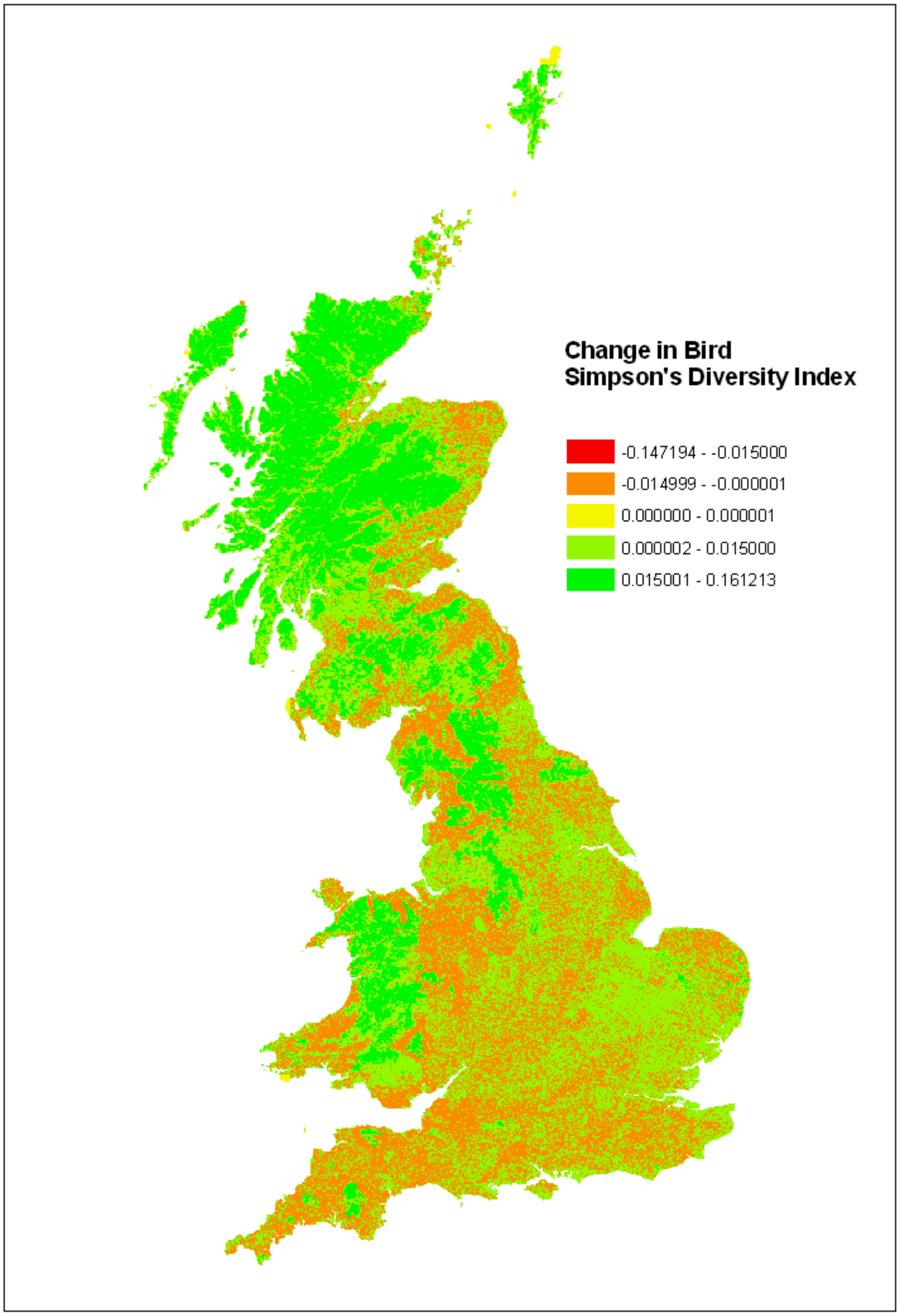

Fig. 1 i) NW Low

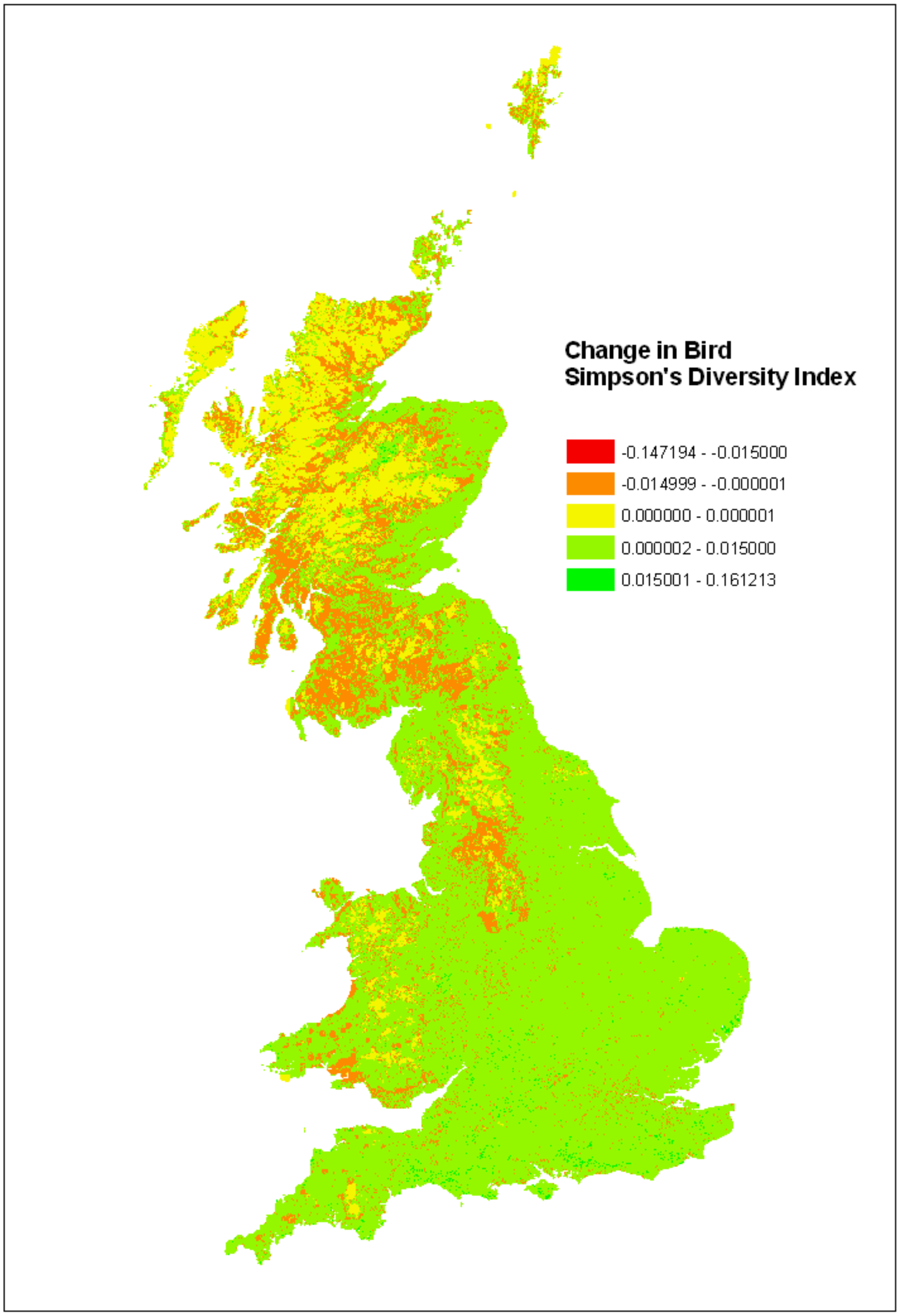
Change in Bird
Simpson's Diversity Index
-0.147194 - -0.015000
-0.014999 - -0.000001
0.000000 - 0.000001
0.000002 - 0.015000
0.015001 - 0.161213

Fig. 1 j) NW High

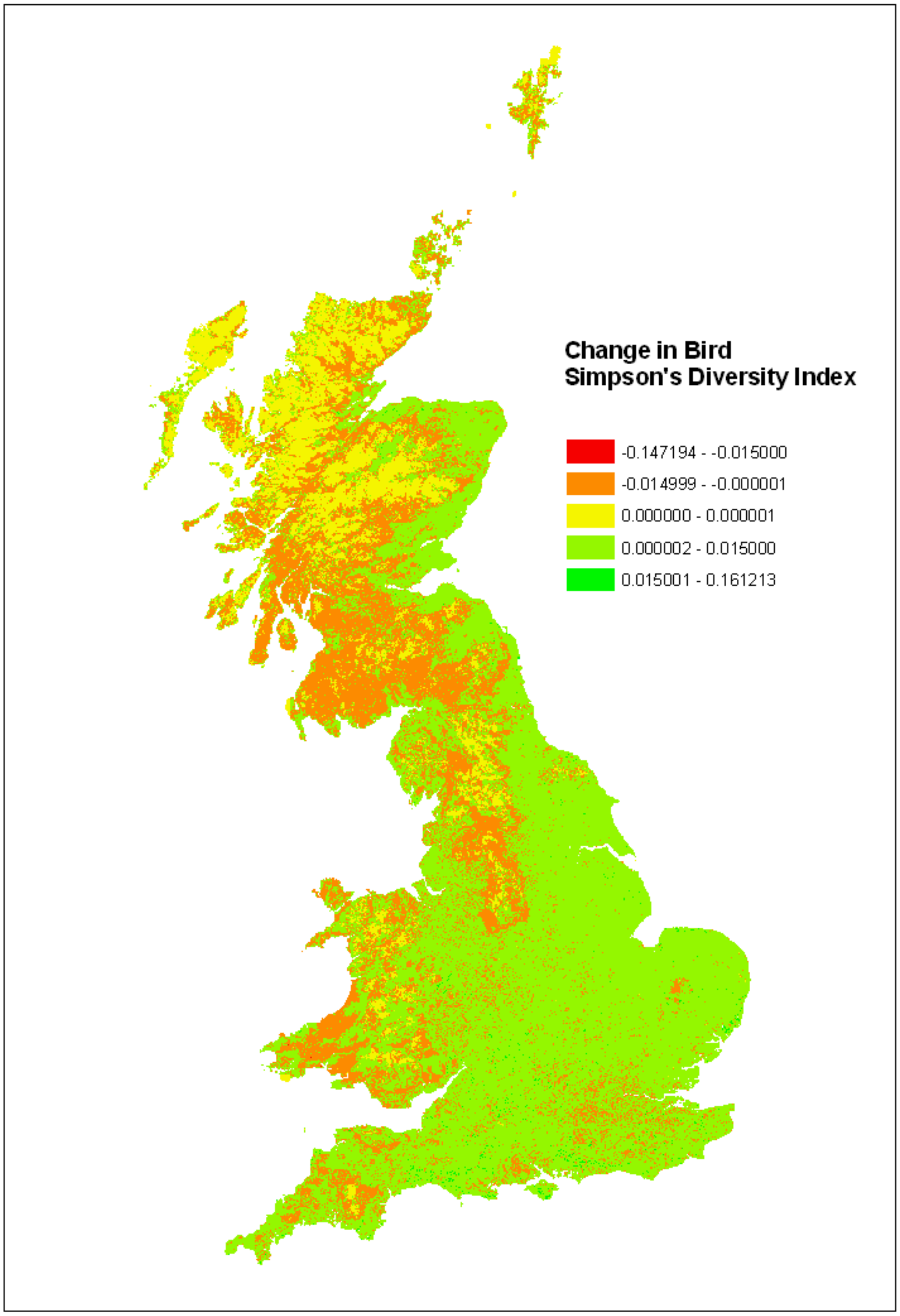

Fig. 1 k) WM Low

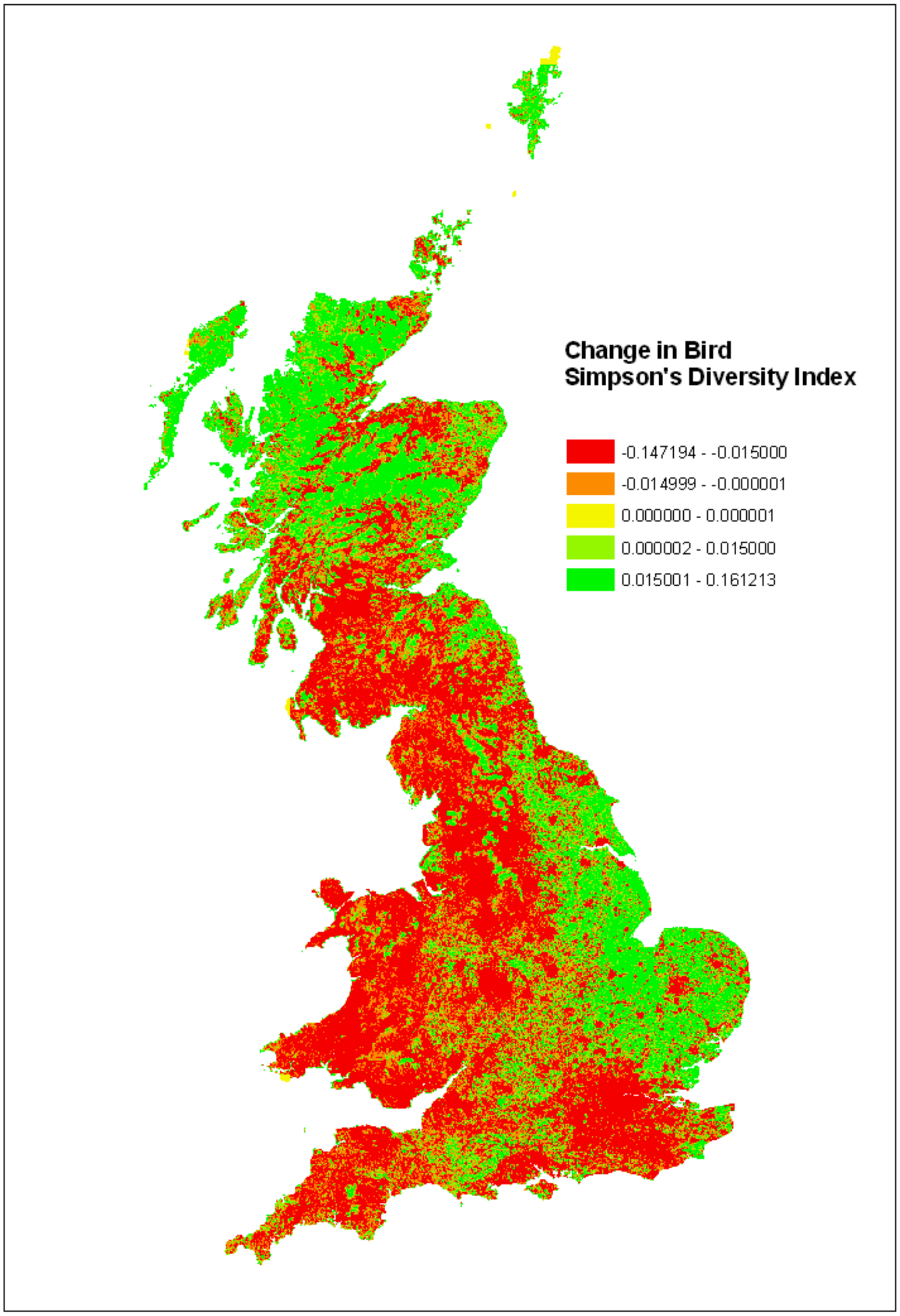
Change in Bird
Simpson's Diversity Index
-0.147194 - -0.015000
-0.014999 - -0.000001
0.000000 - 0.000001
0.000002 - 0.015000
0.015001 - 0.161213

Fig. 1 l) WM High

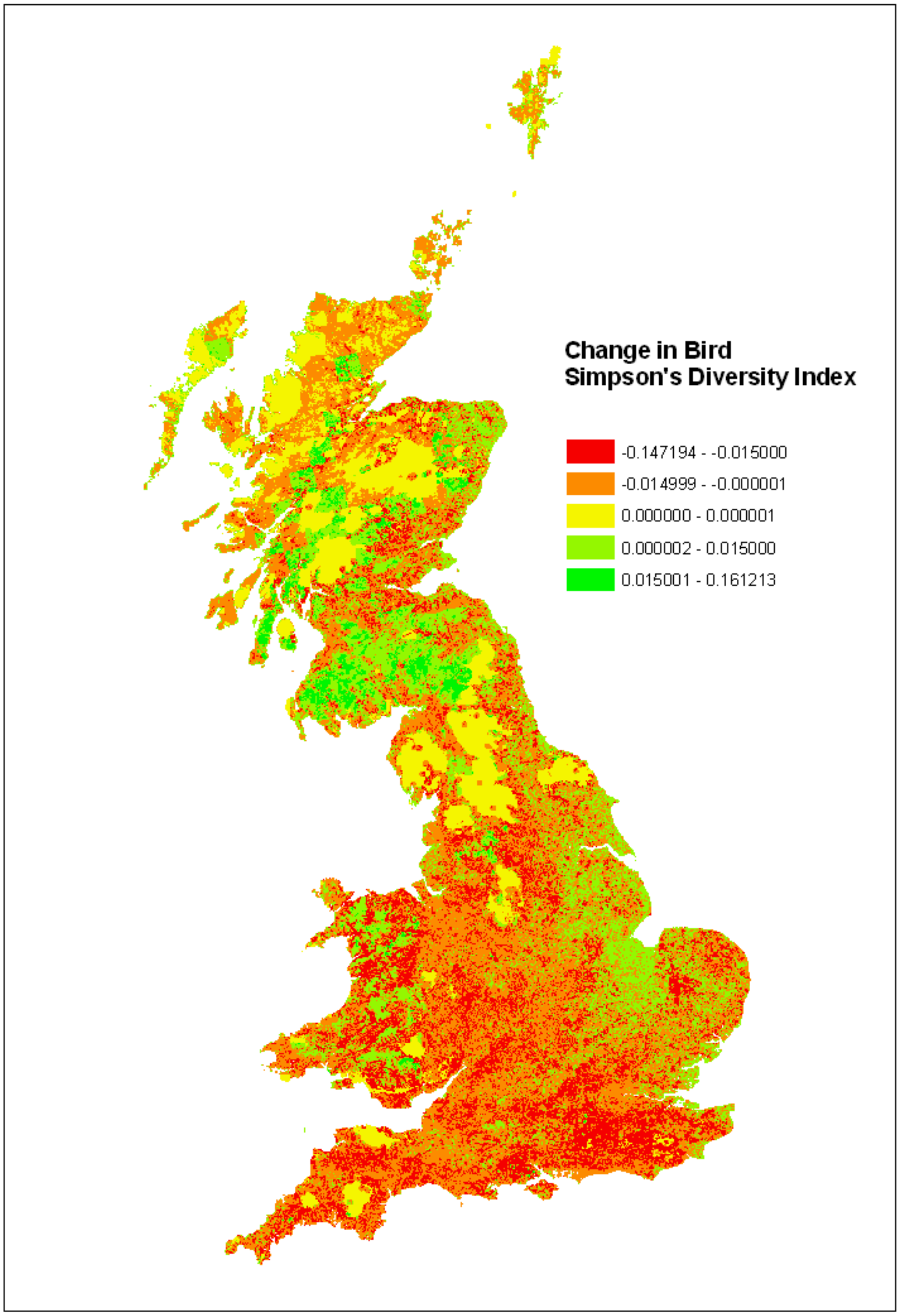

Figure 1. Maps showing predicted change in Simpson's Diversity Index for birds commonly observed on BBS squares between predicted values from the CEH Land Cover 2000 values and predicted values based on 6 scenarios each with a low and high climate model: a, b: Go With the Flow (GF), c, d: Green and Pleasant Land (GPL), e, f: Local Stewardship (LS), g, h: National Security (NS), i, j: Nature at Work (NW) and k, l: World Markets (WM).

Across all scenarios, the minimum change predicted was -0.131 and the maximum change predicted 0.040 (both for WM high). The patterns of change predicted under each of these scenarios are summarized in Table 1. To illustrate what the predicted changes may mean in terms of real changes in the bird community, the diversity for one high-diversity, lowland square in south-east England and one low-diversity, upland square in Scotland was calculated for the year 2000, altering bird numbers slightly to show their effect on the diversity index. The lowland square had 26 species in 2000, including 15 blackbirds, one blackcap, eleven chaffinches, 16 great tits and 37 wood pigeons, giving a diversity index of 9.087. Removing the blackcap resulted in a reduction of 0.123 in the index, removing all eight species with only one individual resulted in a reduction of 0.953, removing one chaffinch reduced the index by 0.043 and redistributing the total number of individuals as if all 26 species had been recorded in equal numbers seen increased the index by 16.913. The upland square had four species, comprising six golden plovers, 24 meadow pipits, one red grouse and two skylarks, giving a diversity index of 1.765. Removing the red grouse reduced the index for the upland square by 0.103, removing one of the golden plovers reduced the index by 0.075, removing one of the meadow pipits reduced the index by 0.0351 and removing 14 meadow pipits reduced the index by 0.795. Most of these fictional changes are outside the minimum-to-maximum ranges predicted under any of the scenarios (Table 1), which all represent changes in absolute diversity values that are well below 10%. Thus, all of the changes predicted would represent, in practice, rather minor changes in bird communities, such as losses or gains of a few individuals of a species, rather than local extinctions or colonizations.

Table 5. Summary statistics showing the changes in bird diversity from the 2000 baseline predicted under each NEA scenario for 2060. All statistics are summaries across all 235,974 1km squares in Great Britain for which mapped predictions were available and so represent the average changes across the whole country and the variability in these patterns.

	Scenario	Statistic								
		Mean	SD	SE	Min	Q1	Median	Q3	Max	Range
Low Climate Change	GF	0.00141	0.00262	0.00001	-0.00480	0.00000	0.00054	0.00220	0.01689	0.02169
	GPL	0.00684	0.00570	0.00001	-0.01561	0.00097	0.00654	0.01172	0.02880	0.04441
	LS	-0.00080	0.00348	0.00001	-0.01424	-0.00237	0.00000	0.00116	0.00777	0.02200
	NS	0.01034	0.01213	0.00002	-0.00722	0.00093	0.00442	0.01864	0.04681	0.05403
	NW	0.00557	0.00556	0.00001	-0.00552	0.00078	0.00432	0.00852	0.03199	0.03751
	WM	0.00019	0.00465	0.00001	-0.02124	-0.00211	0.00020	0.00286	0.01085	0.03209
High Climate Change	GF	0.00175	0.00271	0.00001	-0.00774	0.00000	0.00118	0.00336	0.01526	0.02300
	GPL	0.00467	0.00497	0.00001	-0.01995	0.00000	0.00372	0.00879	0.02577	0.04572
	LS	-0.00024	0.00369	0.00001	-0.01541	-0.00203	0.00015	0.00195	0.01057	0.02598
	NS	0.00870	0.01154	0.00002	-0.01477	0.00022	0.00327	0.01522	0.03838	0.05315
	NW	0.00396	0.00519	0.00001	-0.00959	0.00000	0.00243	0.00659	0.03032	0.03992
	WM	-0.00434	0.01215	0.00003	-0.12531	-0.00735	-0.00087	0.00139	0.02533	0.15064

Discussion

The model presented suggests that much of the variation in the bird diversity index calculated here can be explained by variation in land-use, as measured by the Land Cover Map 2000, together with a control for geographical variation at a regional scale. Accordingly, changes in predicted land cover values due to land use change can be used to predict changes in overall diversity within a square.

All maps of the implications of the NEA scenarios for birds display *changes* in predicted diversity from the current situation, as revealed by models of land-use. Estimates of diversity were derived from models of a diversity index for 1km survey units, rather than as emergent values from species-specific distributions, and the models included a control for geographical location to take account of variation in large-scale distributions that was not accounted for by the broad habitat classification available. In practice, the numerical effect of location on diversity was much larger than those of the land cover variables and the changes in diversity predicted with land cover change are, relatively, very small. This was probably inevitable because bird distributions are influenced by multiple, complex factors and both the habitat categories and bird distribution measure available here were rather coarse. Thus, considerable habitat-related variation in bird diversity is certain not to have been detected by the models and the approach of using a control for regional location is conservative with respect to detecting significant relationships between land-cover and habitat.

Given the above, the maps of bird diversity change for the scenarios (Fig. 1) can be considered to be conservative indicators of the diverse effects of the changes in land cover predicted under each scenario. Within the overall pattern of only small predicted changes in bird diversity, there are quite large differences in the diversity values predicted under each scenario and with low and high predicted climate change (Fig. 1, Table 1).

Before attempting to interpret the maps in detail, it is important to recognise that predicted increases in a diversity index do not necessarily represent conservation "wins" (or, indeed, that predicted reductions are "bad"). The model results indicate the different effects predicted from changes in different land cover classes, based on habitat associations with diversity index values. Increases in relatively high diversity habitats at a cost to lower diversity ones will lead to predicted increases in overall diversity; hence any predicted northward spread of higher diversity habitat (e.g. deciduous woodland) due to climate change will tend to increase diversity in the north. Crucially, however, a diversity index in itself does not specify which species contribute to predicted increases or decreases in diversity: common generalist and rare specialist birds contribute to the index in the same way. In particular, lower diversity areas, such as uplands, support many species of greater conservation concern and an increase in diversity there might well indicate the loss of the local, specialist community and replacement by more common, generalist species. Such a change underlies the predicted increases in upland bird diversity under the National Security and World Markets scenarios in Fig. 1 (d,f,j,l). Conversion of heathland to suburban housing or farmland would lead to a similar increase in diversity and loss of specialist species. Overall, the most "positive" patterns from a biodiversity perspective would probably show a preponderance of "no change" (i.e. yellow in Fig. 1) because this would often represent a genuine lack of change in species composition (a significant change in community composition is unlikely to produce the same species diversity by chance). Thus, in general, it would be unwise to focus on diversity indices alone in assessing changes in ecosystem condition or to interpret results based on local diversity values as indicative of diversity nationally.

As is clear from Fig. 1, every scenario predicted reductions in diversity in some areas and increases in others. These complex patterns make national summaries of the predicted changes in diversity difficult to make. In addition, it is notable that increases in diversity were rather more common than reductions and that mean, median, first quartile and third quartile changes were all either uniformly or mostly positive. In addition, the most negative changes for each scenario have much smaller absolute values than the most positive ones for the same scenarios. All these patterns suggest that changes in bird diversity are generally likely to be positive, with the exception of World Markets under high climate change, while World Markets under low climate change and Local Stewardship under both climate scenarios predict negligible changes in *average* diversity (although also broad ranges of increase and declines, as for the other scenarios; Table 1). Broadly, the Green and Pleasant Land and Local Stewardship storylines have a biodiversity focus in terms of management aims, while Business as Usual adds a "leaning" towards a biodiversity priority to current trends in land-use (NEA Scenarios chapter). Although Nature at Work has an environmental focus, this consists of ecosystem service provision rather than biodiversity maximization, and the World Markets and National Security storylines do not prioritise the environment at all. Hence, the best outcomes for biodiversity as a whole would be expected to be provided by GPL, LS and BAU and the worst by WM, NS and probably NW. Comparing the ranges of bird diversity increases and decreases, which are represented by a consistent colour scheme across all maps in Fig. 1, there are differences in the changes predicted under each scenario and they broadly support this general pattern for GPL, BAU, NS and WM. The results for LS are more complex and those for NW appear rather more positive than might be expected. These patterns are described in more detail below, but the caveats about the relationship between a bird diversity index and true, national diversity discussed above, as well as the obvious issue that bird diversity is likely to reflect that of other animal and plant groups to different extents, should be considered when interpreting the maps in Fig. 1.

Small increases in diversity were predicted in many lowland regions for the BAU low scenario (Fig. 1a), no change in the uplands and some areas of eastern England and scattered decreases across some other lowland areas. Decreases for this scenario appear to be linked to predicted decreases in broadleaved woodland in areas which already hold little of this habitat. For the high BAU model (Fig. 1g) the patterns are similar but with decreases in the north of England, southern Scotland and western Wales. Some of these differences seem to correlate with a lower decrease in broadleaved woodland predicted for the high climate scenario and possibly differences in grassland cover change in west Wales. Nevertheless, and not forgetting the caveats above about interpreting changes in species richness, the BAU scenario generally seems to be rather benign in terms of predicted changes in bird diversity, especially under low climate change (Fig. 1a). The same is true of the GPL and NW scenarios, with all three tending to show a dichotomy between reductions in bird diversity in the uplands and increases in the lowlands under low climate change (Fig 1a,b,e). Further, they all show broadly the same patterns under high climate change, but with greater polarization between uplands and lowlands (Fig. 1g,h,k). The patterns under each of these scenarios would seem to indicate gains in lowland areas, especially arable areas, as habitats that currently support higher bird diversity spread, but these patterns are countered by reductions in the uplands. Given that the latter changes would probably see the total loss of specialists from the uplands (apparently also without replacement by more diverse communities found today at lower altitudes), the generally benign appearance of the maps is probably misleading in terms of effects on national diversity.

Interestingly, the National Security scenario showed the opposite pattern to the three discussed above, with a similar polarization between uplands and lowlands that is exacerbated by greater predicted climate change, but with more positive changes in the uplands (and fenland in Eastern England) and more negative ones in most lowland farmland (Fig. 1d,j). The latter reflects a reduction in habitat diversity in areas with more productive soil for agriculture, so the prediction probably reflects a genuine biodiversity problem. For the reasons discussed above, however, the predicted increases in the north and the uplands should not be considered to represent a compensatory positive effect on biodiversity.

The same caveat should be considered for the World Markets scenario, which shows, under low climate change, the most negative predictions for lowland and southern diversity, but increases in some upland areas and the lowland arable heartlands (Fig. 1f). The latter probably shows the effect of retaining arable land-use in these regions, while more bird-diverse habitats are lost from other regions. Under high climate change, the WM scenario picture is very different, with greater decreases predicted in the southern half of the UK and generally more of a patchwork of increases and reductions, but uplands and moorlands mostly seeing no (net) change or increases (Fig. 1l). This indicates that the changes in land cover linked to an increased overseas ecological footprint could lead to more dramatic and spatially very different changes to the situation with land-use change under the other scenarios. The lowland pattern probably reflects the spread of less biodiverse habitats under the twin pressures of market forces and environmental change, while the upland ones are likely to show the spread of currently "lowland" communities to higher altitudes, as discussed above.

It may be notable that the greatest difference between low and high climate change scenarios was found for Local Stewardship (Fig. 1c,i). Under low climate change, the patterns are not dissimilar to some of the other scenarios, with an arable-pastoral dichotomy and arable bird diversity apparently faring better, although patterns in the Scottish uplands are also positive (Fig. 1c). In general, these patterns probably show positive predicted changes in diversity where local habitat diversity is increased, i.e. where habitats are currently more heterogeneous. Adding the effect of greater climate change suggests that lowland diversity would tend to fare worse and to feature more of a patchwork of increases and reductions, but that the uplands would then fare much better in terms of bird diversity (Fig. 1i). As above, it would be unwise, however, to interpret these increases as positives for conservation.

The discussion above considers certain caveats about the interpretation of the diversity index predictions, but a number of other issues that are specific to the data sets used for the models presented here should also be considered. First, the data source for bird diversity, the BTO/JNCC/RSPB Breeding Bird Survey, is focused on terrestrial breeding birds and its methods and habitat coverage mean that coastal, estuarine, riverine, aerial feeding and rare bird species are probably under-represented in this analysis (Table 2). In addition, no account is taken of wintering birds, but the UK hosts internationally important populations of a range of species in climate-change-sensitive habitats such as estuaries and saltmarshes (Austin & Rehfisch 2003, Rehfisch et al. 2004). These and other limitations of BBS data for the present purpose are described in more detail in Table 2. In addition, both coarse and subtle changes in habitats that are not detectable by remote sensing could have huge effects on bird communities. For example, choices of crop in arable farmland can greatly affect habitat quality for birds (e.g. Wilson et al. 1996), but land cover data would not recognize a change in habitat unless the land-use changed from arable to something else. Similarly, woodland habitat quality is strongly affected by understory vegetation, which can be changed enormously by subtle environmental changes such as increases in deer density (Fuller & Gill 2001), but the land cover classification would again be unaffected. This should also be borne in mind when assessing the apparent impacts of each scenario on bird diversity: it is likely that the predictions are conservative, both in terms of numerical diversity values and effects on individual species that are masked by the use of a summary measure.

Table 2. Explanation of the caveats (considering the source data and the model used) that should be taken into account when interpreting the maps and summaries of bird diversity predicted under each scenario.

Caveat	Description
1) BBS habitat coverage	BBS surveys focus on terrestrial breeding birds, so coastal and estuarine birds tend to be under-recorded, and they make up only a small proportion of the diversity modelled here. Effects of scenarios on bird diversity in these habitats are likely to be underestimated by the models and are likely to be greatest in winter, when UK wetlands host large flocks of waders and waterfowl.
2) BBS survey methods	Birds which are normally observed in flight, such as swifts, swallows and martins, are likely to be under-recorded due to discarding records of birds in flight and by the BBS protocol because they are more active later in the day, so providing a further limit to the comprehensiveness of the diversity measure used here. In addition, birds such as dipper and kingfisher, which are associated with linear waterways, tend to be under-recorded by area-based surveys
3) Treatment of rare species	The number of species contributing to the diversity index was limited to those that were recorded on average in 40 or more squares per year. This was done in order to limit the presence in the data of uncommon non-breeding species which could increase noise in the data and distort the diversity index calculation, but some rare breeders will also have been excluded, making the diversity index rather conservative.
4) Detection probability and "true" diversity	Variations in the detection probability between species and habitats were not accounted for in the analyses described here, so there is the possibility that variation in diversity may be underestimated if it involves more cryptic species (less easily detected further from the transect line), especially in habitats such as woodland where detection probability drops more steeply with increased distance from the observer, compared to more open habitats. It would be possible to estimate "true" diversity by first converting BBS counts to estimated densities using distance analysis (Buckland et al. 2001), but this is not a simple process and involves a number of debatable assumptions about the nature of the survey data in practice.
5) Species identity and composite indices	Simply calculating bird diversity in a BBS square provides no consideration of the types of species involved or their conservation value. Upland habitats, for example, will contain fewer species than lowland areas but those species may be of greater national and international conservation concern than more widely distributed lowland species. Further, relatively species-poor habitats such as heathland, might be colonized by a larger number of species were they to be converted into farmland, scrub or woodland, but the species concerned will often be common generalists rather than scarce habitat specialists. A lower diversity index in the upland habitats may, therefore, be preferable to a higher one if this results in a more homogenous bird community It has been suggested that increased temperature in upland habitats may result in increased diversity due to bird community homogenisation (Davey et al *in prep*). This also raises a general problem with the scale at which diversity is measured, which must be considered if it is to be used to underlie management decisions: aiming to maximize diversity at a local scale will very often give rise to different recommendations to maximizing it at larger scales.

Table 2, Continued.

Caveat	Description
6) Coverage of the uplands	The number of BBS squares covered in upland habitats is limited due to problems of accessibility for volunteers, so the results for these areas are based on fewer data points than those for the lowlands. The analytical approach based on the stratification of the BBS sample used here takes account of regional sample size in producing national average patterns, tending to interpolate results between frequent data points in the lowlands and to extrapolate more from more scattered data in the uplands. The results for the uplands, therefore, should be viewed with more caution, although key birds breeding on upland such as red grouse, meadow pipit, skylark, golden plover and curlew were all included in the diversity index.
7) Consistency of habitat relationships with scale	Birds may differ in their habitat preferences depending on the scale of the change in habitat. A change at the 1km square scale may differ to a change at the 10km square or regional scale. A bird that depends on a matrix of deciduous woodland and farmland being present may react positively to an increasing percentage of woodland in a 1km square, for example, but may be less common in a 10km square with a high percentage of woodland. The model derived here, as it stands, is assessing only the effect of habitat cover at the 1km square scale, but the larger effect of the 100km square variable suggests that larger-scale factors may be more important than changes in land cover at the relatively fine $1km^2$ scale. The gross land cover variables included here, although significant, were less biologically important as drivers of bird diversity than larger-scale landscape variation.
8) Environmental change outside those in Land Cover categories	The model does not factor in the effect of environmental changes other than the broad-scale land-cover classes derived here. Direct effects of climate, for example, could have major impacts on bird distribution independent of their effects on land-use. Some woodland long-distance migrants have shown recent declines which may be related to climate change (Both et al 2006, 2009) and there is also some evidence of changes in bird community composition as a result of climate change (e.g. Gregory et al. 2009). Otherwise good data to support such relationships is sparse so they are not included in the model.
9) Importance of subtle habitat change	Predictions of the effects of land-use change were limited to changes in the high-level Land Cover Map categories, but important effects on biodiversity could easily occur through more subtle changes in cover. For example, switches between the habitats within the upland class will not be registered as changes in land-use but have been show to be important, for example in relation to changes in short- or long-term grazing management (Pearce-Higgins and Grant 2006; Pearce-Higgins et al 2009). Further, huge changes in the character of the landscape could occur through changes in cropping of arable land (both in terms of the nature and timing of agricultural operations and of the choice of crops), but these differences would be undetectable either spatially or temporally in the high-level Land Cover Map data.

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