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Observed and predicted effects of climate change on species abundance in protected areas

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The dynamic nature and diversity of species' responses to climate change poses significant difficulties for developing robust, long-term conservation strategies. One key question is whether existing protected area networks will remain effective in a changing climate. To test this, we developed statistical models that link climate to the abundance of internationally important bird populations in northwestern Europe. Spatial climate–abundance models were able to predict 56% of the variation in recent 30-year population trends. Using these models, future climate change resulting in 4.0 °C global warming was projected to cause declines of at least 25% for more than half of the internationally important populations considered. Nonetheless, most EU Special Protection Areas in the UK were projected to retain species in sufficient abundances to maintain their legal status, and generally sites that are important now were projected to be important in the future. The biological and legal resilience of this network of protected areas is derived from the capacity for turnover in the important species at each site as species' distributions and abundances alter in response to climate. Current protected areas are therefore predicted to remain important for future conservation in a changing climate.

Conservation planning in a changing climate is problematic because species populations can decrease or even disappear from some areas, increase in others, and expand into new regions beyond their current ranges[1–4]. There has been global concern about how these changes might affect protected area networks, one of the main tools used to reduce biodiversity loss. Previous assessments of climate change risk to these networks have considered either the representativeness of particular habitats or biomes[5,6] or the distributions of species[7–9]. However, to be effective at the species level, protected areas must protect populations large enough to have low extinction risk[10–12]. Many networks therefore define the importance and legal status of sites by the size of the population protected within them[13]. To assess the resilience of such networks to climate change, changes in species abundance, rather than just occurrence, should be modelled. Although this can be achieved for single species and populations using models that incorporate detailed biological realism[14], most networks are selected to protect multiple species[11], making such approaches impractical. Here, we use bioclimate models of abundance[15,16] for 62 species, test their predictive power using 30-year population trend data, and apply the tested models to assess the resilience to climate change of a protected area network, which was established to protect multiple species.

We focus on two internationally important European bird assemblages; breeding seabirds and wintering waterbirds. These two groups have been pivotal to the legal classification of Special Protection Areas (SPAs) in Europe, which were established under EU Birds Directive 2009/147/EC. These sites protect 'the most suitable territories in number and size to ensure the survival and reproduction of both rare and threatened birds in their area of distribution', with similar measures for 'regularly occurring migratory species'. Sites in the UK are designated as SPAs when they contain 1% of national populations (rare or threatened species) or 1% of biogeographic populations (migratory species) and species that reach these levels are known as 'qualifying species'[13]. UK SPAs can also be classified for hosting a total species assemblage of at least 20,000 waterbirds or seabirds. SPAs have been integral to past and current European bird conservation[17]. However, future reductions in population size to below the qualifying thresholds could lead to the legal status of individual sites being challenged, an issue of current policy debate[18–20].

We approached this issue in four stages. We first model geographic variation in the abundance of individual species (both within and outside protected areas), to identify climate–abundance relationships. Second, we tested whether past changes in species' abundances (between 1977 and 2006) can be predicted by these models, given the climate change that took place over the same period. This validation is an important test, to allay the concern that statistical relationships between climate and species abundance may occur by chance[21]. The third stage was to use these validated models to project future abundance within protected areas. This allowed us to evaluate whether future climate change is likely to reduce bird populations in the existing network, enabling us to carry out the fourth stage, to assess the implications for the legal status of sites within the network[13]. Given the current interest in how and where protected areas should be located to maximize their resilience to climate change, we investigate which components of SPA selection criteria confer the greatest network resilience.

Using generalized linear models (GLMs) and generalized additive models (GAMs), we described the relationship between climate and abundance from a wide range of monitored sites across northwestern Europe (Ireland, UK, France and The Netherlands). We used high-quality data for 17 species of breeding seabirds (hereafter 'seabirds') and 45 species of wintering waterbirds (hereafter 'waterbirds'), including many with internationally important populations[13,22] (Supplementary Table 1). For stage one, the climate–abundance models were run for all species from the two assemblages. In stage two, these spatial climate–abundance models were validated by predicting 30-year trends in abundance, given the climatic changes that took place during the study period; the spatial models successfully predicted 56% of the observed variation in temporal population trends between species, when using independent

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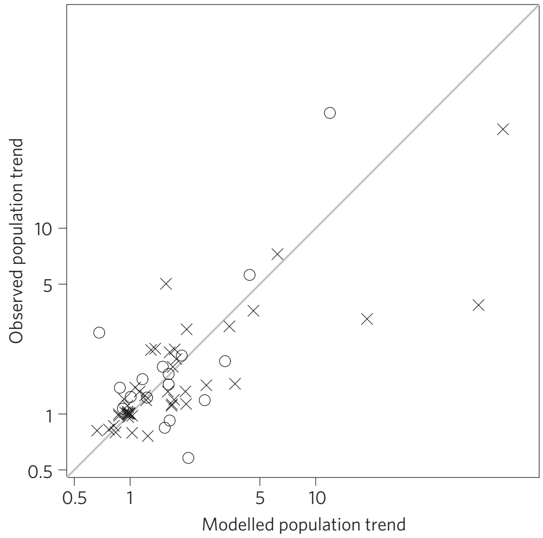

Figure 1 | Model validation of modelled and observed 30-year linear population trends. Population trends calculated across all sites for seabird species (circles) and waterbird species (crosses). Note both axes are on the log scale.

data aggregated across all sites (Fig. 1; $r = 0.75$, $t = 8.803$, $df = 60$, $p < 0.0001$). The magnitude of these correlations exceeds that of previous studies of the impact of recent climate change on bird populations in Europe[23–25]. This suggests that climate change has already been a significant driver of large-scale population trends in both bird assemblages across northwestern Europe, and that these models can therefore be used to project potential future climate change impacts on these populations. Site-specific densities were less well correlated with the modelled estimates, averaging $r = 0.19$ and $r = 0.26$ for seabird and waterbird densities respectively, and the ability of the models to predict site-specific trends averaged $r = 0.12$ for seabirds and $r < 0.01$ for waterbirds. Owing to the uncertainty associated with model projections at individual sites, which may be associated with a combination of non-climatic effects and interactions between climatic and other factors, we focus on results only at the network level.

Many of the species had higher modelled densities in places with cooler, drier summers and warmer winters (Fig. 2). The most important predictor variable was summer temperature (selected in all but one final model), followed by summer precipitation and winter temperature. Interactions between summer precipitation and temperature were significant in 40% of the models, but winter interactions only in 25%. Although seabirds might be more directly affected by sea temperature than the measures of air temperature we used, our models nonetheless had good ability to explain recent large-scale population trends in this group. The apparent sensitivity of seabirds to warming matches empirical observations that describe how recent warming has reduced the abundance and condition of fish prey species for many seabirds[26]. As a result, the productivity of seabirds has declined in some seas[27,28] and the birds may also be directly vulnerable to heat stress[29]. Positive effects of winter temperature on waterbird abundance may reflect improved survival[30,31], whereas negative effects of temperature may operate through variation in prey populations[32].

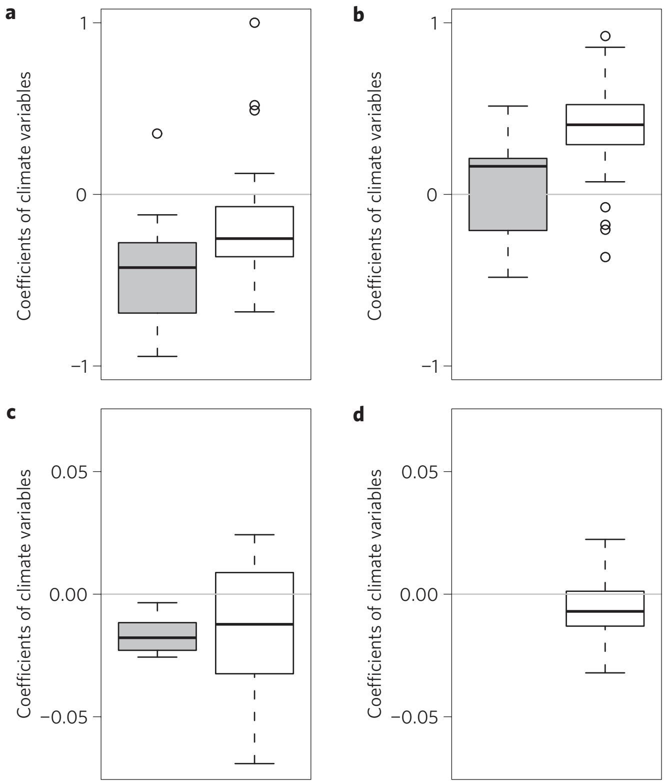

Figure 2 | Marginal linear effects of weather covariates on species abundance. a–d, Box plots of GLM marginal coefficients in final GLMs for summer temperature (**a**), winter temperature (**b**), summer precipitation (**c**) and winter precipitation (**d**), for seabirds (grey) and waterbirds (white). The solid middle line represents the median of coefficients and the box the interquartile range of the coefficients. Whiskers extend to extreme data points and outliers are those points further than 1.5 times the interquartile range from the interquartile range. Marginal coefficients were produced by setting interaction variables at their mean value for a given species data set. No seabird GLMs had significant effects of winter precipitation.

Having validated the climate–abundance models by demonstrating their ability to predict past temporal trends, in stage three we projected future species abundance across the UK SPA network. We used ensemble climate projections for the UK (ref. 33) for emissions scenario A1FI to estimate population trends from the baseline (mean modelled abundance from 1970 to 2000) to 2050 and 2080. As there is inherent spatial variation in abundance that is unrelated to climate, we calculated future abundance estimates by applying the estimated trends to observed site-specific abundances during the baseline period. Future projections were restricted to the UK, thus ensuring they remained as far as possible within the range of climate data used to build the models (Supplementary Fig. 1). As EU Member States have the legal obligation to 'avoid the deterioration of natural habitats and the habitats of species' of their SPAs, this is an appropriate focus, particularly as the UK populations of internationally important breeding seabirds and wintering waterbirds are of high global importance[13,22].

There were projected to be 58% more birds in the entire wintering waterbird assemblage in 2080, but the mean population change was −33% when averaged across species; large population increases for some species were therefore countered by projected declines for most other species (Table 1). The seabird assemblage in 2080 was projected to have 52% fewer individuals and the average projected population trend across species was −44%. The International Union for Conservation of Nature red-list identifies species declining by at least 25 or 50%, for UK amber- and red-listing, respectively[34]. The projected UK population trends suggest that in the future more species may meet these thresholds than those that currently demonstrate the required levels of decline (Table 1). This suggests climate change will threaten the continued persistence of many species in the UK at current population levels.

Using projections of site-specific species abundance based on climate scenarios, in stage four we assessed how many SPAs in the UK network are likely to meet current qualifying thresholds in the future, to test the resilience of the current SPA network and the associated legal framework for site classification. Most seabird and waterbird species were projected to reach current qualifying thresholds on fewer sites in the future (Fig. 3). Overall, we projected a net loss in the number of seabird thresholds reached, with 61 lost and 41 gained by 2080 under the A1FI scenario (Fig. 4). More than half of the seabird sites were projected to lose at least one qualifying species, but about a quarter of these sites were also projected to gain qualifying species (Table 2 and Fig. 5). Ten seabird sites (13%) were projected to lose all qualifying species, but new sites were predicted to more than compensate for these (Table 2). The waterbird assemblage seemed slightly less detrimentally affected, with roughly equal numbers of gains and losses of qualifying thresholds (Fig. 4), although several species were projected to meet qualifying thresholds at no sites in 2080 (Fig. 3). We define turnover in this study as situations in which there are both gains and losses of qualifying species projected, resulting in alteration of the composition of qualifying species within a site. Waterbird sites generally had greater turnover than seabird sites, with all sites losing at least one qualifying species, but most of those also gaining new qualifying species (Fig. 5 and Table 2). For both assemblages, species-rich sites were projected to lose qualifying species, with gains in qualifying species generally projected at sites with few species (Fig. 4).

The qualifying thresholds are set as proportions of national or biogeographical populations. For species that have thresholds based on national populations[13], we also allowed the thresholds to change in accordance with projected changes in national populations (inferred from the changes across the protected area network). By 2080, altered thresholds led to fewer sites losing qualifying species, but also fewer sites gaining qualifying species (Supplementary Table 2). Such change in underlying population size is also likely to occur for those species selected using internationally derived thresholds.

The UK SPA network seems resilient to change; most sites that are important now for individual species or for assemblages are projected to continue to be important in a future changed climate, when assessed using the same criteria. For these results to have general applicability, it is instructive to examine which of the SPA selection criteria contribute most to this resilience. SPAs in the UK may be identified if they support one or more species exceeding 1% of national or biogeographical populations (single-species networks), if they contain multiple qualifying species each attaining the 1% threshold (multi-species networks), or if they contain 20,000 or more individual birds, irrespective of the species (assemblage network). We examined the consequences for network resilience of these three methods of network creation. A single-species strategy would not enable new species to be identified as qualifying species, and therefore no gains in qualifying species could occur. This strategy was projected to result in reductions in the mean number of classified sites per species of 38% (seabirds) and 63% (waterbirds; see Supplementary Note). Alternatively, multi-species sites, which could enable new species to reach qualifying thresholds, would experience only a 9% (seabirds) and 3% (waterbirds) loss of mean sites per species. Assemblage network designation was nearly as effective: 22% and 3% reductions for seabirds and waterbirds, respectively; although for a lower average number of sites per species (Supplementary Note). A multi-species network can, therefore, accommodate turnover and still meet legal designation criteria, as species shift their distributions and abundances in response to climate change[35,36].

Modelling the impact of climate change involves considerable uncertainty[3]. Our approach of modelling abundance has several benefits compared with presence–absence modelling; for example, the interpretation of projections is not dependent on the probability threshold set for occurrence, a significant source of variability for presence–absence modelling[37], and the outputs of abundances are of direct relevance for several policy contexts. However, modelling abundance may exacerbate uncertainty for other reasons. Abundance is a much more finely resolved independent variable than occurrence, and therefore subject to more variation, for example in relation to habitat quality, particularly at fine scales[38]. In addition, modelling abundance also adds statistical challenges, such as a wide range of potential error structures. The data requirements mean that it was not possible to model the rarest species within each assemblage. This may include those particularly vulnerable to climate change, although there is limited evidence for this[23]. The low predictive ability of our models when describing site-based variation in abundance and population trend may in part be a function of some of these difficulties.

The projections assume that the current relationships between climate and abundance are maintained in the future. In addition, both assemblages consist primarily of migratory species that breed or winter elsewhere. Many of the UK's wintering waterbirds breed in boreal or Arctic habitats, and are likely to also be affected by climate change there, whereas seabird survival rates are influenced by climatic conditions across the northeast Atlantic or further afield. As with other studies[1,8], we do not account for these potential large-scale influences on abundance. However, the strong correlation between observed and predicted trends across all sites suggests that the models do provide a good description of national-scale climate change impacts on abundance.

The success of these abundance models at predicting observed population change may be attributable to the statistical power of being able to model, predict and test changes in density throughout species' ranges, rather than being limited to analysing changes at distributional limits when only considering the presence or absence of a species. The abundance models suggest that recent climate change has been a significant driver of breeding seabird and wintering waterbird populations in western Europe over the past 30 years, as supported by specific studies of both groups[27,36,39].

Table 1 | Projected changes to assemblage abundance and the number of species meeting UK red-list and amber-list population decline criteria[34], for two different time periods under the A1FI emissions scenario.

Assemblage	Year	Geometric mean population change	Change in entire assemblage population	Number of species meeting long-term population decline criteria		
				Red-list −50%	Amber-list −25%	Neither
Breeding seabirds	Now			0	3	14
	2050	−22%	−31%	3	3	11
	2080	−44%	−52%	7	0	10
Wintering waterbirds	Now			0	3	42
	2050	−11%	+23%	11	10	24
	2080	−33%	+58%	19	5	21

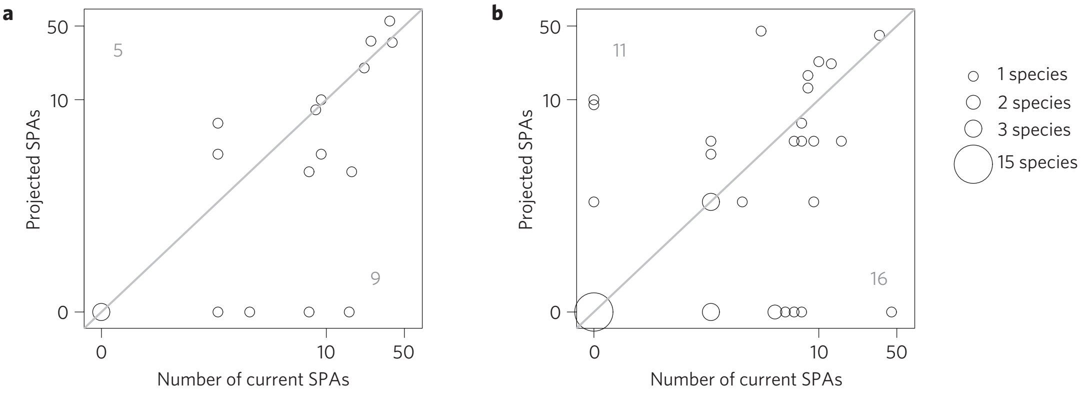

Figure 3 | Projected changes to the representation for each species on current SPAs. a,**b**, The number of current and projected future SPAs under an A1FI emissions scenario in 2080, at which each species reaches qualifying thresholds for breeding seabirds (**a**) and wintering waterbirds (**b**). Circle areas are scaled linearly to the number of species and the legend (which applies to both graphs) shows example sizes. The grey line represents equality, whereby the species is projected to receive equivalent legal protection in future as now. Grey numbers are the total numbers of species either above or below the line, representing those species projected to reach qualifying thresholds at more or fewer sites respectively. Note the log scale of both axes.

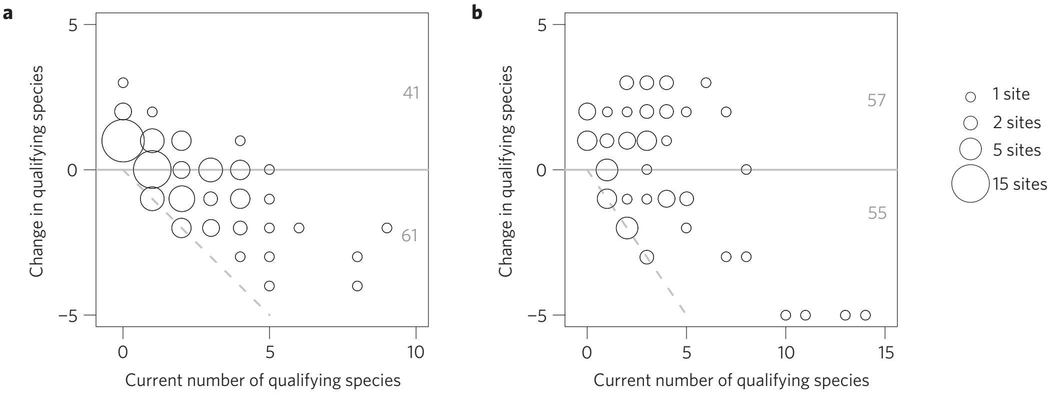

Figure 4 | Projected changes to the number of qualifying species in each current SPA. a,**b**, Scatter plots show changes in numbers of qualifying species per site from now to 2080 under the A1FI scenario for breeding seabirds (**a**) and wintering waterbirds (**b**). SPAs lying on the horizontal solid grey line are not projected to change the number of qualifying species (although they may experience turnover in species identity). Circle areas are scaled linearly to the number of sites and the legend (which applies to both graphs) shows example sizes. The grey numbers represent the total number of sites that have achieved net gains (above solid grey line) and losses (below solid grey line) in the number of species reaching qualifying thresholds. Groups of SPAs on the dotted grey line are those that are projected to lose all their qualifying species.

Table 2 | Table of the number of SPAs that are projected to show a change in the number of qualifying species for two different time periods under the A1FI emissions scenario.

Assemblage	Year	Number of sites with changes to qualifying species					
		No change	Turnover				New sites
			Only gain	Gain and lose	Only lose	(Lose all)	
Breeding seabirds	2050	33	11	7	27	(4)	16
	2080	25	12	8	33	(10)	23
Wintering waterbirds	2050	0	0	40	17	(10)	6
	2080	0	0	42	15	(11)	7

'Turnover' refers to sites that already have at least one qualifying species and gain and/or lose other qualifying species. Sites losing all qualifying species are listed in brackets, as they are a subset of sites that are losing qualifying species. New sites are those that are already SPAs (by alternative criteria), now with no individual species at a qualifying threshold, but are projected to have qualifying species in the future.

By incorporating data from outside the UK when producing our models, we were able to capture most of the likely future range in climate at these sites, even under the A1FI 2080 scenario (Supplementary Fig. 1), although future climate change may result in increasingly divergent ecological processes to those currently operating in particular locations or climates[40].

Although climate change threatens the effectiveness of the protection now afforded birds within existing individual protected areas[8,20,41], we do not find evidence that it will substantially alter the efficacy of the UK's SPA network for conserving breeding seabirds and wintering waterbirds, assuming the administrative process for site identification and designation keeps pace with bird population

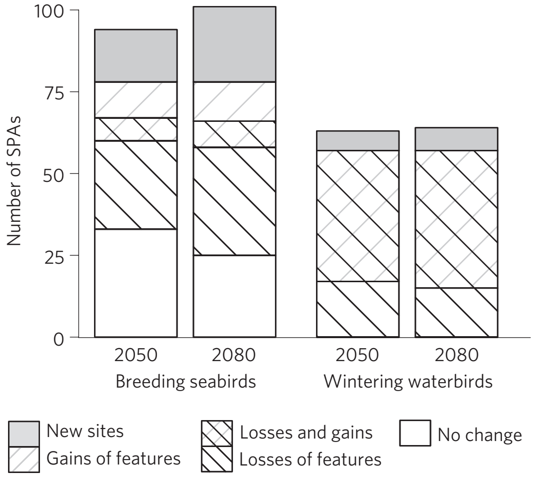

Figure 5 | Projected changes to the species qualifying within SPAs for each assemblage. Bar plots indicate the number of SPAs with current seabird or waterbird classifications based on abundance thresholds, which are projected to gain or lose qualifying species from now to 2050 and 2080 under the A1FI emissions scenario.

changes. Most SPAs are likely to continue to support at least some species at current qualifying population sizes, suggesting the network will continue to protect significant populations of these species groups in the future. Losses of qualifying species at some sites are likely to be compensated by increases for the same species at other sites, as also suggested for African protected areas[7]. This resilience of the network to climate change is further facilitated by the flexibility in the current system for classifying sites on the basis of the proportion of the national or biogeographical population they hold[18], an approach adopted for other global protected areas[42] enabling designations to adapt to large-scale population changes[43]. Studies examining networks based on habitat representativeness have found that many networks are robust to climate change[5,44] and the UK SPA network may implicitly protect a representative range of habitats, by selecting protected areas for a range of species.

The resilience of the network is due in part to the ability of species that have declined below qualifying thresholds in some sites, to increase and reach qualifying thresholds in other sites. The ability for protected sites to accommodate future turnover is therefore a key component of a resilient network. This capacity for turnover in species will also depend on a distribution of sites that is geographically dense enough that there is good provision of alternative sites for species to reach qualifying thresholds on, if they drop below qualifying thresholds at their original sites. It also requires regular assessment of the network and associated updating of the lists of species for which individual sites are classified.

The apparent resilience of the protected area network does not mean that the network will protect each species from climate change impacts. Indeed, our models suggest that 41% of the breeding seabirds and 53% of the wintering waterbirds we assessed may suffer population declines of greater than 25% in the UK under an A1FI scenario by 2080, as a result of climate change impacts alone. However, any negative impacts on populations within protected areas may be less negative than impacts in the surrounding landscape. Given this and other uncertainties and assumptions in the modelling and projections, a precautionary approach to protected area selection would provide greater contingency against unpredicted impacts of climate change on populations.

To conclude, there has been much discussion about the continued efficacy of protected areas as the climate changes[8,18–20]. Our results, which to our knowledge are the first to model the effects of climate change on population size of an assemblage of species across a national protected area network, suggest that the existing UK SPA network will remain viable during the next 70 years of climate change by continuing to protect large numbers of breeding seabirds and wintering waterbirds. Although this will not intrinsically protect certain species and assemblages from all impacts of climate change, and the assemblage composition at each site may alter, these sites will continue to be locations where some vulnerable populations will be retained. Our results indicate that to maximize the resilience of protected area networks to future climate change, they should be extensive, multi-species or multi-habitat networks with considerable capacity for turnover between sites. Using flexible classification criteria, for example identifying sites that support a threshold proportion of a regional or global population[13], will further increase the legal resilience of sites to future change. Extensive protected area networks designated using large numbers of species are therefore shown to be robust conservation instruments in a dynamic climate.

Methods

Data sources. Bird abundance data for individual sites in northwestern Europe from 1966 to 2006 (Supplementary Table 3) were used to construct abundance–climate relationships. Sufficient data were obtained to model the abundance of 17 seabird and 45 waterbird species that comprise most of the 23 seabird and 51 waterbird species that were used to classify UK SPAs (ref. 13). Bird counts were summed within spatial units that varied by region and species group; either 25 km squares, quarter degree grid cells, or French departments.

Climatic variables[33,45] were chosen to include known descriptors of European bird distributions[1]; temperature of the warmest summer month, temperature of the coldest winter month, and total precipitation in winter and summer. Moisture availability was described by interactions between temperature and precipitation within each season. Summer was defined as June–August for waterbirds and species-specific breeding seasons for seabirds[46,47]. Winter was defined as December–February for all species. Measures of summer and winter climate were included in models for all species, to account for any effects of climate mediated by habitat quality or food availability[27].

Modelling methods. Density was modelled as abundance in each spatial response unit, offset by the log of the total area of the site(s) from which the counts originated. For waterbirds, total site area was used, and for eight cliff-nesting seabirds, total cliff length in that spatial response unit. For the seabird species not associated with cliffs for nesting, models were necessarily of abundance rather than density. Covariates were the four climate variables, two interactions and an elevation variable. An appropriate error structure was selected for each species and minimum adequate models selected from the full model using backwards stepwise selection. All modelling was carried out in R (ref. 48). See Supplementary Methods for full details of the data and modelling.

Model validation. Three assessments were made of the predictive ability of the final models, each of which was conducted using 10-fold cross-validation[49]. The two fine-scale validations were the strength of the correlation between the observed and predicted densities and changes in densities at each site. As impacts of climate change may be better validated at large scales[24], we compared observed and predicted population change, aggregated across all SPAs.

Future projections. Future species projections were made using climate projections for emissions scenario A1FI, which equates to an increase in global mean temperature of 2.8 and 4.4 °C, by 2050 and 2080, respectively[33]. Projections were presented for change from the most recent 30-year time period in the observed bird data, and were an average of the GLM and GAM projections. The climate projections rely on emissions and climatic scenarios, which themselves have a number of associated caveats[50], which we do not discuss here. Projected bird densities described likely mean densities for a given climate, irrespective of site quality. Therefore, to account for existing spatial heterogeneity in site and/or habitat quality, the projected trend was multiplied by the observed density at each site. To estimate abundance this was then multiplied by site area. There is no equivalent information on site and/or habitat quality for currently unoccupied sites and so this approach cannot predict colonizations. Although we therefore assumed no range expansion[8], as many SPAs contained a small number of individuals of several species, there was substantial opportunity for significant and large population increases to be projected by the models, even when excluding completely new colonizations. In addition, to prevent inappropriately high future projections of abundance due to density dependence, we capped the maximum projected densities at the 99.5th quantile of observed densities[15].

We assessed projected future abundance against the current SPA qualifying threshold for each species, and examined for each SPA whether it was projected to continue to support populations of sufficient size to merit current classification, and for how many species. This provides a fixed metric of change and means that our results can be easily compared with the present. For Annex I species, SPA thresholds were identified with reference to national population size. For these species, we additionally allowed qualifying threshold size to vary in proportion to total abundance across all SPAs to reflect the flexibility inherent in SPA classification.

We assessed climate changes from 'now' (1977–2006) to 2050 and 2080 under the A1FI scenario, which describes the maximum (but increasingly likely) amount of change now projected within the given time frames. To identify the most vulnerable species, we applied conservation listing criteria to these population trends, estimating the projected number of species likely to meet UK amber-list and red-list decline criteria in the future, by those projected to decline by at least 25% or 50%, respectively, over at least a 25-year period[34].

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Author contributions

A.J., J.W.P-H. and C.D.T. wrote the article, with significant input from M.A., A.M.D., R.B.B., D.E.C. andF.J., and all other authors contributed to the manuscript. A.B., H.P., M.M.R., D.E.C., A.J., J.P.H., A.M.D., M.A., F.J., R.B.B. and C.D.T. designed the study. A.J., N.O., C.B.T. and S.E.N. ran models and analysed results. A.J., S.R., B.C., A.S.C.P.C., O.C., B.D., M.H., F.J. and N.O. collated and prepared data. D.A.S., R.A.M., A.D., A.B., H.Q.P.C. and H.P. provided scientific advice throughout the project.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to A.J.

Competing financial interests

The authors declare no competing financial interests.

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