UNIVERSITÀ DEGLI STUDI DI TORINO

This is an author version of the contribution published on:
Questa è la versione dell'autore dell'opera:
Nature Climate Change, 3: 1055-1061, 2013, doi:10.1038/nclimate2035

The definitive version is available at:
La versione definitiva è disponibile alla URL:
http://www.nature.com/nclimate/journal/v3/n12/full/nclimate2035.html

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

Authors, Affiliations & Contacts:

*Alison Johnston, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK, alison.johnston@bto.org

Malcolm Ausden, Reserves and Protected Areas Department, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK, malcolm.ausden@rspb.org.uk

Andrew M. Dodd, Reserves and Protected Areas Department, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK, andrew.dodd@rspb.org.uk

Richard B. Bradbury, Conservation Science Department, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK, richard.bradbury@rspb.org.uk

Dan E. Chamberlain, DBIOS, Università di Torino, Via Accademia Albertina 13, 10123 Torino, Italy, dan.chamberlain99@gmail.com

Frédéric Jiguet, UMR7204 MNHN-CNRS-UPMC, Muséum National d'HistoireNaturelle, CRBPO, CP 51, 55 rue buffon, 75005 Paris, France, fjiguet@mnhn.fr

Chris D. Thomas, Department of Biology, University of York, Heslington, York, YO10 5DD, UK, chris.thomas@york.ac.uk

Aonghais S.C.P. Cook, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK, aonghais.cook@bto.org

Stuart E. Newson, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK, stuart.newson@bto.org

Nancy Ockendon, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK, nancy.ockendon@bto.org

Mark M. Rehfisch, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK, Now at: APEM Limited, Wellington House, East Road, Cambridge, CB1 1BH, UK, m.rehfisch@apemltd.co.uk

Staffan Roos, British Trust for Ornithology Scotland, School of Natural Sciences, Cottrell Building, University of Stirling, Stirling, FK9 4LA, UK, Now at: Royal Society for the Protection of Birds, 2 Lochside View, Edinburgh Park, EH12 9DH, UK, staffan.roos@rspb.org.uk

Chris B. Thaxter, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK, chris.thaxter@bto.org

Andy Brown, Natural England, TouthillClose,City Road, Peterborough, PE1 1UA, UK, andy.brown@naturalengland.org.uk

Humphrey Q.P.Crick, Natural England, Eastbrook, Shaftesbury rd, Cambridge, CB2 8DR, UK, humphrey.crick@naturalengland.org.uk

Andrew Douse, Scottish Natural Heritage, Great Glen House, Leachkin Road, Inverness, IV3 8NW, UK, andy.douse@snh.gov.uk

Rob A. McCall, Countryside Council for Wales/CyngorCefnGwladCymru, Welsh Assembly Government Building, RhodfaPadarn, LlanbadarnFawr, Aberystwyth, Ceredigion, SY23 3UR, UK, r.mccall@ccw.gov.uk

Helen Pontier, DEFRA, Zone 1/05B, Temple Quay House, Temple Quay, Bristol, BS1 6EB, UK., helen.pontierMCIWEM@defra.gsi.gov.uk

David A. Stroud, Monkstone House, City Road, Peterborough, Cambridgeshire PE1 1JY, UK, david.stroud@jncc.gov.uk

Bernard Cadiou, GISOM, c/o Bretagne Vivante - SEPNB, 186 rue Anatole France, BP 63121, F-29231 BREST cedex 3, France, bernard.cadiou@bretagne-vivante.org

Olivia Crowe, BirdWatch Ireland, 20D Bullford Business Campus, Kilcoole, Co. Wicklow, Ireland, ocrowe@birdwatchireland.ie

Bernard Deceuninck, Ligue pour la Protection des Oiseaux, FonderiesRoyales - BP 90263 17305 Rochefortcedex, France, bernard.deceuninck@lpo.fr

Menno Hornman, Sovon Dutch Centre for Field Ornithology, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands, menno.hornman@sovon.nl

James W. Pearce-Higgins, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK, james.pearce-higgins@bto.org

The dynamic nature and diversity of species' responses to climate change pose significant difficulties for developing robust long-term conservation strategies. One key challenge is whether existing, static protected area networks will remain effective in a changing climate. To test this, we developed statistical models linking climate to the abundance of internationally important bird populations in northwestern Europe. The models described 56% of the variation in recent 30-year population trends. Using these models, future climate change was projected to cause 25% or greater declines in population of more than half of the species considered. However, a protected area network in the UK was predicted to retain sufficient species abundances to maintain the legal status of most sites, with sites that are important now continuing to be important in the future. This network resilience derived from the multi-species and assemblage criteria used to classify protected areas, which allow for turnover and colonisation of sites by species as their distributions shift. Current protected areas should continue to be a primary focus of conservation action to increase species and network resilience to climate change.

Conservation planning under climate change 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 by conservationists to prevent biodiversity loss. Previous assessments of climate change risk to these networks have considered either the presence or 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 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. Whilst this can be achieved for single species and populations using models that incorporate much biological realism[14], most networks are selected to protect multiple species[11], making such approaches impractical. Instead, we can utilise recent extensions to bioclimate modelling approaches that allow abundance to be modelled [1516].

We apply these methods to assess the resilience to climate change of a protected area network established to protect multiple species, focussing on two internationally important European bird assemblages; breeding seabirds and wintering waterbirds. These two groups have been pivotal to the legal designation of Special Protection Areas (SPAs) in Europe, which were established under EU Birds Directive 2009/147/EC to 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 are designated as SPAs when they contain 1% of national or biogeographic populations, and species which reach these levels are known as 'qualifying species'[13]. Sites can also be designated for containing a total species assemblage of at least 20 000 birds. Although SPAs have benefitted wild bird populations in the past[17], future changes to population sizes within the network could lead to populations within sites dropping below the 1% thresholds, even if species are not lost completely from a given site, potentially threatening the legal status of individual sites, an issue of current policy debate[18–20].

We approach this question in three 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 test 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 is to use these validated models to project future abundance within protected areas. This allows us to evaluate whether future climate change is likely to reduce wild bird populations in the existing network, in order to assess the legal and policy implications [13]. Given the current interest in how and where protected areas should be located to maximise their resilience to climate change, we investigate which components of SPA selection criteria confer the greatest network resilience.

Using GLMs and GAMs, we describe the relationship between climate and abundance from a wide-range of monitored sites (SPAs and non-SPAs) across western Europe (Ireland, UK, France and the Netherlands; countries for which comparable data were available) for 17 species of breeding seabirds (hereafter "seabirds") and 45 species of wintering waterbirds (hereafter "waterbirds"), including many internationally important populations[13,22] (Supplementary Table 1).The climate-abundance models fit the data well at a large spatial scale; modelled 30-year trends in abundance describe 56% of observed variation in population trends between species, when using independent data aggregated across all sites (Figure 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, at this spatial scale, climate change has already been a significant driver of large-scale population trends in both assemblages across Western Europe, and that these models can therefore be used to project potential future climate change impacts upon 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, whilst the ability of the models to predict site-specific observed trends averaged r=0.12 for seabirds and $r<0.01$ forwaterbirds. Thus at the scale of individual sites, the majority of variation was not attributable to climate, but to more localised factors. Due to this uncertainty associated with model projections at individual sites, we focus on results at the network level.

Many of the species had higher modelled densities in places with cooler, drier summers and warmer winters (Figure 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 which describe how recent increases in sea-surface temperature have reduced the abundance and condition of fish prey species for many seabirds[26]. As a result, the productivity of seabirds has declined in relation to warmer temperatures[27,28] and they may also be vulnerable to more direct negative effects of warming through heat stress[29]. Positive effects of winter temperature upon waterbird abundance may reflect improved survival[30,31], whilst negative effects of temperature may operate through variation in prey populations[32].

After validating that the climate-abundance models adequately described observed trends at a large spatial scale, and using the relationships between climate and abundance identified in the models, we projected future species abundance across the UK SPA network. We used ensemble climate projections for the UK[33] for emissions scenario A1FI to estimate population trends from the baseline (mean predicted abundance from 1970 - 2000) to 2050 and 2080. We applied these estimated trends to observed site-specific abundance for the baseline period, in order to produce projections that account for inherent spatial variation in species' abundance between sites that is unrelated to climate. Future projections to test the resilience of the SPA network to climate change were restricted to the UK, thus ensuring they remained as far as possible within the range of climate data used to build the models. As it is nation states which have a legal obligation to maintain the favourable status of their SPAs, this is an appropriate focus, particularly as the UK populations of the internationally important breeding seabird and wintering populations that we consider are of high global importance[13,22].

There were projected to be 58% more birds in the entire waterbird assemblage in 2080, but the mean population change was -33% when averaged across species; large population increases for some species were countered by projected declines in abundance for the majority of 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%. An increasing number of both waterbird and seabird species were projected to exceed the 50% or 25% population decline thresholds for red or amber-listing criteria[34] (Table 1), suggesting climate change will threaten the continued persistence of many species at current UK population levels.

Using projections of site-specific species abundance based on climate scenarios, we assessed how many SPAs in the UK network will meet current qualifying thresholds in the future, in order to test the resilience of the current legal framework underpining SPAs. The majority of both seabird and water bird species were projected to reach qualifying thresholds on fewer sites (Figure 3). Overall, there was a projected net loss of the number of seabird thresholds reached, with 61 lost and 41 gained by 2080 under the A1FI scenario (Figure 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 (Figure 3, Table 2). 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 appeared slightly less detrimentally affected, with roughly equal numbers of gains and losses of qualifying thresholds (Figure 4), although several species were projected to meet qualifying thresholds at no sites in 2080 (Figure 3). Waterbird sites generally had greater turnover than seabird sites, with all sites losing at least one qualifying species, but most of those also gaining qualifying species (Figure 5, Table 2). For both assemblages, gains in the number of qualifying species were projected in sites with few species, with species rich sites projected to lose qualifying species (Figure 4).

The qualifying thresholds are set as proportions of national or biogeographical populations. For species which 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).

The SPA network appears resilient to change; the majority of sites which are important now for individual species or for assemblages will continue to be important under a future changed climate, when assessed using the same criteria. It is instructive to examine which of the SPA selection criteria contribute most to this resilience, for these results to have general applicability. Firstly, SPAs may be identified if they support 1 % of national or biogeographical populations of a species. Were this classification just applied to a single species, the resulting network would have reduced resilience to change for that species, compared to one classified for a multiple species. Greater losses are projected at the species-level compared to the combined, multiple species network, where species can gain qualifying status at new sites currently protected for other species (Supplementary material Appendix 1). A combined species network can therefore better accommodate turnover, already demonstrated as important for wintering waterbirds showing rapid distribution shifts in response to recent warming[35,36]. Alternatively, the network could focus on the sites supporting the largest populations (likely to be the biggest and best-quality sites) which, in the case of SPAs, are those which qualify on the assemblage criterion. Doing so would result in a network with good resilience to change, but with many fewer sites protected, with reduced potential for sites that currently support relatively small populations to become more important through time (Supplementary material Appendix 1). The SPA network therefore appears resilient to change primarily because species can increase in abundance at protected sites (designated for other species) where they don't currently reach qualifying thresholds.

Modelling the impact of climate change involves considerable uncertainty[3]. Our approach of modelling abundance has several benefits compared to presence-absence modelling; for example, the interpretation of projections is not dependent upon 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 the European policy context. 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 these difficulties, although this did not appear to differ systematically between cliff-nesting and other seabirds, which were modelled with different levels of information on habitat availability.

The projections assume that the current relationships between climate and abundance remain in the future. Additionally, both assemblages consist primarily of migratory species which breed or winter elsewhere. Many of the wintering waterbirds breed in boreal or Arctic habitats further north, and are likely to be impacted by climate change there, whilst seabird survival rates are influenced by climatic conditions across the north-east 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 of each assemblage.

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' distributions, rather than being limited to analysing changes at distribution margins 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 last 30 years, as supported by specific studies of both groups [27,36]. By incorporating data from outside the UK when producing our models, we were able to capture most of the likely future variation in climate at these sites, even under the A1FI 2080 scenario (Supplementary Figure XX), although future climate change may result in increasingly divergent ecological processes to those currently operating in particular locations or climates[39].

Although climate change threatens the effectiveness of the protection currently afforded birds within existing individual protected areas[8,18,40], we do not find evidence that it will substantially reduce the efficacy of the SPA network in the UK for conserving breeding seabirds and wintering waterbirds. The majority of SPAs will continue to support at least some species at current qualifying thresholds, suggesting the network will continue to protect large populations of these species groups in the future. Losses of qualifying species at some sites are likely to be compensated by increases at other sites, as also suggested for African protected areas[7]. This resilience of the network to climate change is further enhanced by the flexibility in the current system for classifying sites on the basis of the proportion of the national or biogeographical population they hold[19], enabling designations to adapt to large-scale population changes.

This apparent resilience of the protected area network does not mean that the network will protect each species from the impacts of climate change. Our models suggest that 41 % of breeding seabirds and 53 % of wintering waterbirds assessed may suffer projected population declines of greater than 25% in the UK under an A1FI scenario by 2080, as a result of climate change impacts alone. Instead, our results suggest that these sites, which are sensible locations within which to target conservation action for these species now, will remain important foci for such conservation management in the future. Additionally, any negative impacts on populations within protected areas may be less negative than impacts in the surrounding landscape, particularly as local management has the potential to increase the resilience of populations to detrimental impacts of climate change (Pearce-Higgins 2011). The weak correlations between observed and predicted densities and trends at the fine-scale support this, indicating that the local condition of individual sites, which is amenable to improvement through management, is a much more important driver of bird populations than climate at this scale, whilst climate-change impacts are better detected at a large scale. Overall, a precautionary approach should be taken to ensure that networks of protected areas have sufficient contingency to protect species and assemblages in the future, particularly given the large uncertainties.

Some previous studies of the likely impacts of climate change upon protected areas based on species' occurrence have suggested that that new policies are required to adapt protected areas to climate change[8,18], whilst others suggest that existing networks may be adequate[10]. The SPA network is targeted at a wide range of species, and therefore implicitly protects a wide range of habitats, selecting for each species the sites with the largest populations. At the network level, if not at the site level, it appears resilient to climate change impacts. This result concurs with some studies considering networks of protected areas based on habitat representativeness[5,41]. It is clear that the most resilient networks will protect a range of sites important for a wide-range of species, and by doing so, provide high-quality sites for potential colonisation by range expanding species[9,42].

To conclude, there has been much policy discussion about the efficacy of protected areas in a changing climate[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 protected area network will remain viable during the next 70 years of climate change by continuing to protect large numbers of breeding seabirds, wintering waterbirds and their habitats. Although this will not intrinsically protect certain species and assemblages from climate change, and the assemblage composition at each site may change, these sites will continue to be the priority locations where conservation action in response to climate change should be targeted in order to increase the resilience of vulnerable populations. The multi-species and assemblage criteria of SPA classification provide the underpinning flexibility for this, which allow for species turnover at the site level, and should be applied to other protected area networks.

Methods

Data sources

Bird abundance data for individual sites in the UK, Ireland, France and the Netherlands from 1966-2006 were collated (Supplementary Table 3) to enable us to construct abundance-climate relationships over a wide a range of climates and so maximise the ability of our models to describe future climatic conditions in the UK. For each species, we required data from at least two countries and in at least two time periods, and sufficient data were obtained to model the abundance of 17 seabird and 45 waterbird species which comprise the majority of the 23 seabird and 51 waterbird species which were used to classify UK SPAs[13]. Site-specific abundances of waterbirds in January were averaged over non-overlapping five-year periods to eliminate the consequences of short-term fluctuations and to account for lagged climate effects. They were also summed within 25 km squares (in the UK) or quarter degree grid cells (elsewhere), to reduce the potential impacts of spatial autocorrelation. Visual inspection of semi-variograms revealed no substantial autocorrelation at this scale. Seabird abundance data from the UK, Ireland and France represented totals from discrete survey periods and were similarly summed across 25 km squares, or French departments (as site-specific estimates were unavailable for France).

Monthly climatic data were obtained for the UK at a 25 km^2 resolution[33], and for Europe at a quarter degree resolution[43]. The climate variables used in the analysis were chosen to include known descriptors of European bird distributions - summer warmth, winter cold, and moisture availability[1]: mean minimum temperature of the coldest month, mean maximum temperature of the warmest month, mean maximum temperature of the warmest month during the breeding season, total winter precipitation, total summer precipitation and maximum monthly breeding season precipitation. Summer was defined as June-August, winter as December-February, and we used species-specific breeding seasons[44,45]. Interactions between temperature and precipitation in each season were also included to describe moisture availability. Due to collinearity in the summer and breeding season variables, seabirds were modelled with the winter and breeding season variables, and waterbirds were modelled with the winter and summer variables. Hereafter “summer” refers to the summer period for waterbirds and the species-specific breeding period for seabirds. Measures of summer and winter climate were included in models for all species, to account for any effects of climate mediated by habitat or food[27]. In order to ensure that the two datasets were equivalent, we compared UK and European climate data within the UK. There were strong correlations with all variables ($r>0.91$in all cases). However to maximise the coherence, we used the slope of the relationships to calibrate the two datasets.

The average elevation within each response unit (25 km squares, quarter degree cells or French departments), and within each site was calculated[46]. To account for topographic effects on local climate, the models included, as an explanatory variable, the difference between the mean elevation of the response unit, and the mean elevation of the sites within that unit, weighted by site area. For eight cliff-nesting seabirds (*Alca torda*, *Fratercula arctica*, *Uria aalge*, *Fulmarus glacialis*, *Rissa tridatyla*, *Morus bassanus*, *Phalacrocorax aristotelis* and *P. carbo*), the availability of suitable nesting habitat in the UK and Ireland was estimated from the cliff length within each spatial response unit. This was defined using a digital elevation model[47], as land with a slope of >18° within 50m of the high water mark, excluding areas with a height < 10m.

Modelling Methods

Abundance was modelled as a function of four climate variables and two interactions, as described above. The density of waterbirds was modelled using abundance in each response unit, offset by the log of the area of the site(s) from which the counts originated. The density of cliff-nesting seabirds was modelled using abundance within each response unit, offset by the log of cliff length in that unit. An additional dummy variable was included describing the interaction between cliff length and country because cliff length data were unavailable for France. For the remaining seabird species, models were necessarily of abundance rather than density.

Given the variable nature of the bird data, we could not *a priori* determine an appropriate error structure for all species. Saturated GLMs and GAMs were therefore run with multiple error distributions: Poisson, over-dispersed Poisson, negative binomial, zero-inflated Poisson, zero-inflated negative binomial and, for breeding seabirds due to their extremely skewed count data, the Tweedie distribution of errors[48]. The best-fitting distribution was selected for GLMs and GAMs separately, by examination of residuals and standard model fit diagnostics, and this distribution was then used during final variable selection.

Minimum adequate models for each species were selected from a full model using backwards stepwise selection and at least one of the following variable assessment criteria, depending upon the final error distribution and model used: t-test (exclusion threshold $p>0.05$), F-test (exclusion threshold $p>0.05$), AIC ($\Delta AIC>0$) and/or GCV ($\Delta GCV>0$). GAM one-dimensional smooths had a maximum of four degrees of freedom, with eight applied to two-dimensional (interaction) smooths. To reduce over-fitting, the gamma parameter was set at 1.4 and each non-parametric relationship was visually examined to check for biological plausibility. Where required, the degrees of freedom were reduced. We used the final GLM models to identify the most important predictor variables for both assemblage groups, as the linear terms within the model structures are simpler to summarise than the GAMs. All modelling was carried out in R[49]; see the supplementary material for further details.

Model Validation

Three assessments were made of the predictive ability of the final models; a fine-scale spatial validation, a fine-scale temporal validation, and a large-scale temporal validation. All validations were based on 10-fold cross-validation, in which random 10% samples are removed from the modelling and their values correlated with predictions from models based on the other 90% of the data. Final predictions were made from the average of the GLM and GAM models, unless their predictive ability differed by $r>0.125$, in which case projected abundances were from the better fitting model. Validations included the strength of the correlation between the observed and predicted densities and change in densities. Recognising that impacts of climate change may be better validated at large rather than fine-scales[24], we additionally aggregate for each species the predicted population change across all SPAs and compare that to the observed change.

Future Projections

Future species projections were made using climate projections for emissions scenario A1FI, which roughly equates to a 4°C increase in global mean temperature, from the end of the 20th century to the end of the 21st century[50]. Projections were presented for the median prediction of change for 2050 and 2080 and "current", which refers to the most recent 30-year time period which was available in the data (for waterbirds 1976-2006, and for seabirds an average of the two surveys). Although using only the median climatic predictions limits the probabilistic scope of the projections, the climate projections do not account for the collinearity between variables, which when using models with multiple variables, may be unrealistic. The projections rely on these climatic scenarios, which themselves have a number of associated caveats, which are not discussed further here[51]. Projected 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. To estimate abundance this was then multiplied by site area:

$$\widehat{N}_{i,t2} = \mathrm{A} \cdot D_{obs,i,t1} \left(\frac{D_{mod,i,t2}}{D_{mod,i,t1}} \right)$$

Where $\widehat{N}_{i,t2}$ is the estimated abundance at site i in future time period $t2$, A is the site area, D is density, either modelled (D_{mod}) or observed (D_{obs}), at site i in time period t, where $t1$ is current.

This approach estimates abundance given the current quality of that site relative to other sites. There is no equivalent information, however, about site quality for currently unoccupied sites and so this approach cannot predict colonisations. In common with other authors[8], we therefore assume no range expansion. As many SPAs contain a small number of individuals of a species, there is substantial opportunity for significant and large population increases to occur, even when excluding completely novel colonisations. Additionally, in order 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 within the original data[15].

We compare $\widehat{N}_{i,t2}$ against the current SPA qualifying threshold for each species, and assess for each SPA whether it is 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 our results can be easily compared to the present. However, this does not accurately reflect the flexibility inherent in the SPA classification process, within which population thresholds are set at 1% of the national or biogeographical populations. If changes in national populations are equivalent to biogeographic populations, then we would project more gains and more losses than would occur. However, if national population changes are different to biogeographical populations, then there will be biases in our projected changes. It is very difficult to model biogeographical populations, and therefore we maintain this assumption. We additionally examined the consequences for the predictions of applying this change in threshold for Annex I species by allowing national population size, and therefore threshold size, to vary in proportion to total abundance across all SPAs. Annex I species are particularly rare, vulnerable or threatened and for these reasons are listed on Annex I of the EC Birds Directive (2009/147/EC). As we did not model abundance across the entire biogeographical or flyway population, this same assessment was not possible for non-Annex I migratory species.

We take change in the following ways: from “current” (1977-2006) to 2050 and 2080 under the A1FI scenario, which describes the maximum (but now likely) amount of change currently projected within the given time frames. In order to identify the most vulnerable species, we apply current 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].

References

1. Huntley, B., Green, R. E., Collingham, Y. C. & Willis, S. G. *A Climatic Atlas of European Breeding Birds*. (Lynx Edicions, 2007).
2. Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333,** 1024–1026 (2011).
3. Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. Impacts of climate change on the future of biodiversity. *Ecology Letters* **15,** 365–377 (2012).
4. Devictor, V. *et al.* Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change* **2,** 121–124 (2012).
5. Ferrier, S., Harwood, T. & Williams, K. J. *Using generalised dissimilarity modelling to assess potential impacts of climate change on biodiversity composition in Australia, and on the representativeness of the National Reserve Sytem.* (A report prepared for the Department of Sustainability, Environment, Water, Population and Communities, 2010).
6. Lemieux, C. J. & Scott, D. J. Climate change, biodiversity conservation and protected area planning in Canada. *The Canadian Geographer/Le Géographe canadien* **49,** 384–397 (2005).
7. Hole, D. G. *et al.* Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters* **12,** 420–431 (2009).
8. Araújo, M. B., Alagador, D., Cabeza, M., Nogues-Bravo, D. & Thuiller, W. Climate change threatens European conservation areas. *Ecology Letters* **14,** 484–492 (2011).
9. Thomas, C. D. *et al.* Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences* **109,** 14063–14068 (2012).
10. McCarthy, M. A., Thompson, C. J. & Possingham, H. P. Theory for designing nature reserves for single species. *American Naturalist* **165,** 250–257 (2005).
11. McCarthy, M. A., Thompson, C. J. & Williams, N. S. G. Logic for designing nature reserves for multiple species. *American Naturalist* **167,** 717–727 (2006).
12. McCarthy, M. A., Thompson, C. J., Moore, A. L. & Possingham, H. P. Designing nature reserves in the face of uncertainty. *Ecology Letters* **14,** 470–475 (2011).
13. Stroud, D. A. *et al. The UK SPA Network: Its Scope and Content*. (JNCC, 2001).
14. Peery, M. Z., Gutiérrez, R. J., Kirby, R., LeDee, O. E. & LaHaye, W. Climate change and spotted owls: potentially contrasting responses in the Southwestern United States. *Global Change Biology* **18,** 865–880 (2012).
15. Renwick, A. R., Massimino, D., Newson, S. E., Pearce-Higgins, J. W. & Johnston, A. Modelling changes in species' abundance in response to projected climate change. *Diversity and Distributions* **18,** 121–132 (2012).
16. Huntley, B., Altwegg, R., Barnard, P., Collingham, Y. C. & Hole, D. G. Modelling relationships between species spatial abundance patterns and climate. *Global Ecology and Biogeography* **21,** 668–681 (2012).
17. Donald, P. F. *et al.* International conservation policy delivers benefits for birds in Europe. *Science* **317,** 810–813 (2007).
18. Cliquet, A., Backes, C., Harris, J. & Howsam, P. Adaptation to climate change: legal challenges for protected areas. *Utrecht Law Review* **5,** 158–175 (2009).
19. Dodd, A. M., Hardiman, A., Jennings, K. & Williams, G. Protected areas and climate change: reflections from a practitioner's perspective. *Utrecht L* **6,** 141–150 (2010).
20. Dodd, A. M. *et al.* Protected areas and wildlife in changing landscapes: the law and policy context for NGO responses to climate change in the UK. *Journal of International Wildlife Law and Policy* **15,** 1–24 (2012).
21. Beale, C. M., Lennon, J. J. & Gimona, A. Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences* **105,** 14908–14912 (2008).

22. Mitchell, P. I., Newton, S. F., Ratcliffe, N. & Dunn, T. E. *Seabird Populations of Britain and Ireland*. (T. & A.D. Poyser, 2004).
23. Green, R. E. *et al.* Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters* **4,** 599–602 (2008).
24. Gregory, R. D. *et al.* An Indicator of the Impact of Climatic Change on European Bird Populations. *Plos One* **4,** (2009).
25. Jiguet, F. *et al.* Population trends of European common birds are predicted by characteristics of their climatic niche. *Global* **16,** 497–505 (2010).
26. Daunt, F. *et al.* The impact of the sandeel fishery closure on seabird food consumption, distribution and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Science* **65,** 362–381 (2008).
27. Frederiksen, M., Edwards, M., Mavor, R. A. & Wanless, S. Regional and annual variation in black-legged kittiwake breeding productivity is related to sea surface temperature. *Marine Ecology Progress Series* **350,** 137–143 (2007).
28. Riou, S. *et al.* Recent impacts of anthropogenic climate change on a higher marine predator in western Britain. *Marine* **422,** 105–112 (2011).
29. Oswald, S. A., Bearhop, S., Furness, R. W., Huntley, B. & Hamer, K. C. Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas Catharacta skua. *Journal of Avian Biology* **39,** 163–169 (2008).
30. Piersma, T., Rogers, K. G., Boyd, H., Bunskoeke, E. J. & Jukema, J. Demography of Eurasian Golden Plovers Pluvialis apricaria in The Netherlands, 1949-2000. *Ardea* **93,** 49–64 (2005).
31. Kéry, M., Madsen, J. & Lebreton, J. D. Survival of Svalbard pink-footed geese Anser brachyrhynchus in relation to winter climate, density and land-use. *Journal of Animal Ecology* **75,** 1172–1181 (2006).
32. Van de Pol, M. *et al.* Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology* **91,** 1192–1204 (2010).
33. Murphy, J. M. *et al. UK Climate Projections Science Report: Climate Change Projections*. (Met Office Hadley Centre, 2009).
34. Eaton, M. A. *et al.* Birds of conservation concern 3: the population status of birds in the United Kingdom, Channel Islands and the Isle of Man. *British* **102,** 296–341 (2009).
35. Maclean, I. M. D. *et al.* Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Global Change Biology* **14,** 2489–2500 (2008).
36. Lehikoinen, A. *et al.* Rapid climate driven shifts in wintering distribution of waterfowl. *Global Change Biology* **19,** 2071–2081 (2013).
37. Nenzén, H. K. & Araújo, M. B. Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* **222,** 3346–3354 (2011).
38. Gaston, K. J. & Lawton, J. H. Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos* **58,** 329–335 (1990).
39. Walther, G.-R. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365,** 2019–2024 (2010).
40. Hannah, L. *et al.* Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* **5,** 131–138 (2007).
41. Dunlop, M. & Brown, P. R. *Implications of climate change for Australia's National Reserve System: a preliminary assessment*. (Department of Climate Change, 2008).
42. Hiley, J. R., Bradbury, R. B., Holling, M. & Thomas, C. D. Protected areas act as etablishment centres for species colonizing the UK. *Proceedings of the Royal Society - Series B* **280,** 1760 (2013).
43. Haylock, M. R. *et al.* A European daily high-resolution gridded dataset of surface temperature and precipitation. *Journal of Geophysical Research* **113,** D20119 (2008).
44. Crick, H. Q. P., Dudley, C., Glue, D. E. & Thomson, D. L. UK birds are laying eggs earlier. *Nature* **388,** 526 (1997).

45. Snow, D. & Perrins, C. M. *The Birds of the Western Palaearctic (Concise Edition)*. (Oxford University Press, 2004).
46. Jarvis, A., Reuter, H. I., Nelson, A. & Guevara, E. Hole-filled seamless SRTM data v4. International Centre for Tropical Agriculture (CIAT). (2008). at <http://srtm.csi.cgiar.org>
47. O.S. *OS Landform PANORMA*. (2011).
48. Dunn, P. K. & Smyth, G. K. Evaluation of Tweedie exponential dispersion model densities by Fourier inversion. *Statistical Computing* **18,** 73–86 (2008).
49. R Development Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation for Statistical Computing, 2012).
50. I.P.C.C. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. (Cambridge University Press, 2007).
51. Jenkins, G. *et al. UK Climate Projections: Briefing Report. Version 2*. (Met Office Hadley Centre, 2010).

Acknowledgements

We would like to thank all those professional and amateur ornithologists who contributed to the collection of bird data. We also acknowledge the provision of bird data from a variety of different regions including the UK, Ireland, France and the Netherlands, which included schemes coordinated or contributed to by BirdWatch Ireland, British Trust for Ornithology, Countryside Council for Wales, Environment and Heritage Service for Northern Ireland, Groupement d'Intérêt Scientifique Oiseaux Marins, International Waterbird Census, Joint Nature Conservation Committee (JNCC), Ligue pour la Protection des Oiseaux, National Parks and Wildlife Service, Natural England, Royal Society for the Protection of Birds, Scottish Natural Heritage, SOVON Dutch Centre for Field Ornithology and Wildfowl and Wetlands Trust. Weather data were provided by UKCP09 and E-OBS from the EU-FP6 project ENSEMBLES, and future climate projections were from UKCP09. Other data was provided by International Centre for Tropical Agriculture, Ordnance Survey and JNCC. We acknowledge input from Graham Austin, Ian Burfield, Niall Burton, Colin Campbell, Nigel Clark, Greg Conway, David Fouracre & Simon Wotton.

Author Contributions: AJ, JPH and CDT wrote the artice, with significant input from MA, AMD, RBB, DEC & FJ, and all other authors contributed to the manuscript. AJ, DEC, MMR, JPH, AMD, MA, FJ, RBB & CDT designed the study. AJ, NO, CBT & SN ran models and analysed results. AJ, SR, BC, ASCPC, OC, BD, MH, FJ& NO collated and prepared data. DAS, RAM, AD, AB, HQPC & HP provided scientific advice throughout the project.

Competing Financial Interests Statement

No competing financial interests are reported.

Table 1: Table indicating the number of species in each assemblage currently meeting and projected to meet UK red-list and amber-list population decline criteria[34] at 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%	None
Breeding seabirds	Currently			0	3	14
	2050	-22%	-31%	3	3	11
	2080	-44%	-52%	7	0	10
Wintering waterbirds	Currently			0	3	42
	2050	-11%	+23%	11	10	24
	2080	-33%	+58%	19	5	21

Table 2: Table of the number of SPAs which are projected to lose all the qualifying species in two different time periods under the A1FI emissions scenario. ‘Turnover’ refers to sites which 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 which are losing qualifying species. New sites are those which are already SPAs (by alternative criteria), currently with no individual species at a qualifying threshold, but are projected to have qualifying species in the future.

Assemblage	Year	Number of sites with changes to qualifying species					
		No change	Turnover				New sites
			Gain only	Gain & lose	Lose only	(Lose all)	
Breeding seabirds	2050	33	11	7	27	(4)	16
	2080	25	12	8	33	(10)	23
Wintering waterbirds	2050	0	0	40	18	(10)	6
	2080	0	0	43	15	(11)	7

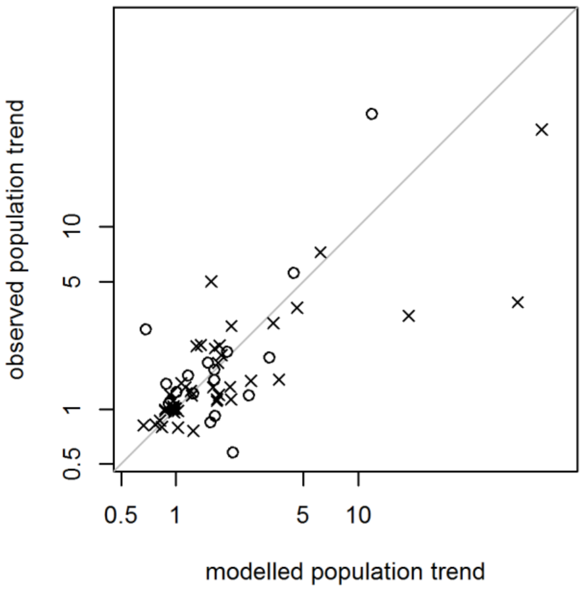

Figure 1: Plot of the modelled linear 30-year population trend (1977-2006) for each species across all sites, and the observed linear 30-year population trend across all sites for seabird species (○) and waterbird species (×). Note both axes are on the log scale.

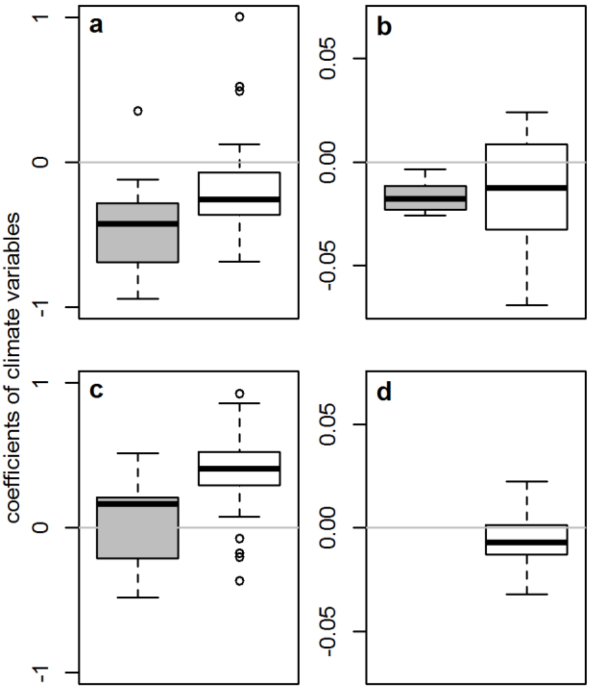

Figure 2: Boxplots of GLM marginal coefficients in final models for a) summer temperature; b) summer precipitation; c) winter temperature; and d) winter precipitation, for seabirds (grey) and waterbirds (white). Marginal coefficients were produced by setting interaction variables at their mean value for a given species dataset. No seabird GLMs had significant effects of winter precipitation.

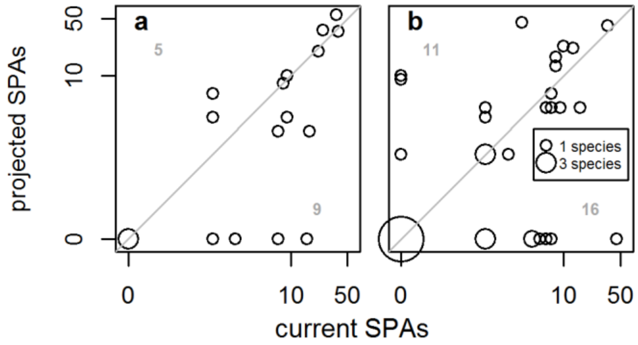

Figure 3: The number of current and projected future SPAs under an A1FI emissions scenario to 2080, at which each species reaches qualifying thresholds for a) breeding seabirds and b) wintering waterbirds. The area of each dot represents the number of species and the grey line the line of equality. Grey 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 on the axes.

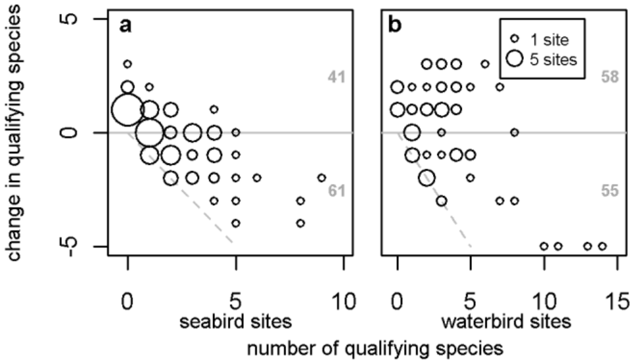

Figure 4: Scatterplots of the change in number of qualifying species per site from current to 2080 under the A1FI scenario to 2080 shown for a) breeding seabirds and b) wintering waterbirds. SPAs lying on the solid grey line are not projected to change the number of qualifying species (although may have turnover in species identify). SPAs on the dotted grey line are those which are projected to lose all their qualifying species. The area of each dot represents the number of sites with those projected changes. The grey numbers represent the total number of sites which have achieved net gains (above solid grey line) and losses (below solid grey line) in the number of species reaching qualifying thresholds.

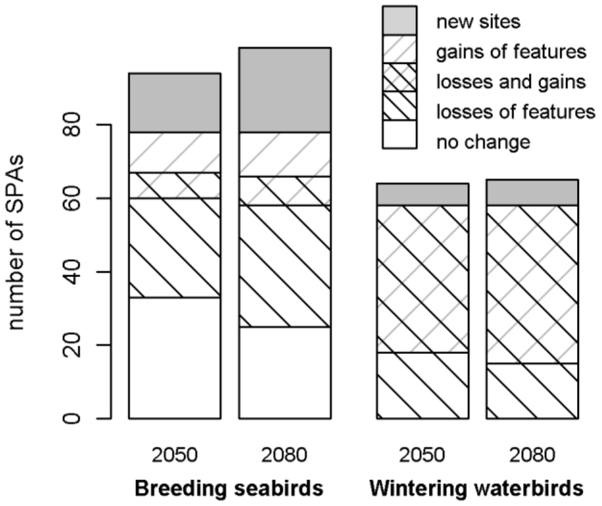

Figure 5: Barplots indicate the number of SPAs with current seabird or waterbird classifications based on abundance thresholds, which are projected to gain or lose qualifying species from now to 2050 and 2080 under the A1FI emissions scenario.