The effectiveness of protected areas to conserve species undertaking geographic range shifts.

Phillipa K. Gillingham[1, 2]

Richard B. Bradbury[3]

David B. Roy[4]

Barbara J. Anderson[2, 5]

John M. Baxter[6]

Nigel A. D. Bourn[7]

Humphrey Q. P. Crick[8]

Richard A. Findon[9]

Richard Fox[7]

Aldina Franco[10]

Jane K. Hill[2]

Jenny A. Hodgson [11]

Alison R. Holt[12]

Mike D. Morecroft[13]

Nina J. O'Hanlon[2]

Tom H. Oliver[4]

James W. Pearce-Higgins[14]

Deborah A. Procter[15]

Jeremy A. Thomas[16]

Kevin J. Walker[17]

Clive A. Walmsley[18]

Robert J. Wilson[19]

Chris D. Thomas[2]

[1]Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Talbot Campus, Fern Barrow, Poole, BH12 5BB, United Kingdom

[2]Department of Biology, Wentworth Way, University of York, YO10 5DD, United Kingdom

[3] RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Beds, SG19 2DL, United Kingdom

[4]NERC Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, United Kingdom

[5] Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand

[6]Policy & Advice Directorate, Scottish Natural Heritage, Silvan House, 231 Corstorphine Road, Edinburgh, EH12 7AT, United Kingdom

[7]Butterfly Conservation, Manor Yard, East Lulworth, Dorset, BH20 5QP, United Kingdom

[8]Natural England, Eastbrook, Shaftesbury Road, Cambridge, CB2 8DR, United Kingdom

[9]DEFRA, Area 1B, Nobel House, 17 Smith Square, LONDON, SW1P 3JR, United Kingdom

[10]School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich, NR4 7T, United Kingdom

[11]Department of Evolution, Ecology and Behaviour, Biosciences Building, University of Liverpool, Crown Street, Liverpool, L69 7ZB, United Kingdom

[12]Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, United Kingdom

[13]Natural England, Cromwell House, 15 Andover Road, Winchester, SO23 7BT, United Kingdom

[14]British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, United Kingdom

[15]Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough, PE1 1JY, United Kingdom

[16]Department of Zoology, University of Oxford, Oxford OX1 3PS, United Kingdom

[17]Botanical Society of the British Isles (BSBI), c/o 97 Dragon Parade, Harrogate, North Yorkshire, HG1 5DG, United Kingdom

[18]Natural Resources Wales, Maes y Ffynnon, Penrhosgarnedd, Bangor, LL57 2DW, United Kingdom

[19]College of Life and Environmental Sciences, Hatherly Building, University of Exeter, Exeter EX4 4PS, United Kingdom

Corresponding Author: P. Gillingham, Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Talbot Campus, Fern Barrow, Poole, BH12 5BB, United Kingdom. Email: pgillingham@bournemouth.ac.uk

Abstract

A cornerstone of conservation is the designation and management of protected areas (PAs): locations often under conservation management containing species of conservation concern, where some development and other detrimental influences are prevented or mitigated. However, the value of PAs for conserving biodiversity in the long term has been questioned given that species are changing their distributions in response to climatic change. There is a concern that PAs may become climatically unsuitable for those species they were designated to protect, and may not be located appropriately to receive newly-colonising species for which the climate is improving. Here, we analyse fine-scale distribution data from detailed resurveys of seven butterfly species and 11 birds in Great Britain to examine any effect of PA designation in preventing extinctions and promoting colonisations. We found a positive effect of PA designation on species' persistence at trailing-edge warm range margins, with a decreased effect of PA at higher latitudes and altitudes. In addition, colonisations by range expanding species were more likely to occur on PAs even after the effects of altitude and latitude had been taken into account. PAs will therefore remain an important strategy for conservation. The potential for PA management to mitigate the effects of climatic change for retracting species deserves further investigation.

Keywords

Adaptation - Birds – Butterflies – Climate change – colonisation - conservation – extinction – reserves – Site of Special Scientific Interest - SSSI

Introduction

We now have strong evidence that a wide range of species are changing their distributions in response to recent climatic change (e.g. Hickling *et al.* 2006, Chen *et al.* 2011), with some species expanding towards the poles or uphill into areas that have become climatically suitable for those species and other species contracting from areas where the climate has become less suitable for them (e.g. Franco *et al*. 2006, Zografou *et al.* 2014). These range shifts potentially pose a problem for conservationists trying to protect species in static reserves, because reserves at warm range margins are likely to become unsuitable for at least some of the species they were designated to protect (Peters & Darling 1985).

Recent modelling studies have predicted that climatic change will lead to species being lost from some reserves (Araújo *et al.* 2004, 2011, Kharouba & Kerr 2010) and some reserves will experience a high turnover of species in future (Bagchi *et al.* 2013, Hole *et al.* 2009). Some authors have even suggested that dynamic reserves, which track the distributions of species, might be more effective at conserving species than static reserves (Rayfield *et al.* 2008). However, designating dynamic reserves for a variety of different species is impractical, since species respond individualistically to the same level of environmental change (e.g. Mair *et al.* 2012) and in countries with high human pressure such as England, there is not very much natural or semi-natural habitat to be found outside current PAs (Lawton *et al.* 2010). An alternative strategy is to manage existing sites, either to reduce sources of harm not linked to climate (Pearce-Higgins & Green 2014), or to counter the effects of climatic change (e.g. blocking upland drains to retain soil moisture, Carroll *et al.* 2011). These actions could mitigate some of the negative effects of climatic change (Pearce-Higgins 2011) and might allow species to persist in areas where the climate is deteriorating for them. Thus it is important to assess the degree to which existing PAs conserve species under climatic change. In this study we examined whether populations of northerly-distributed, cold-adapted species were less likely to have retracted from PAs, or have taken longer to do so, compared with populations in the surrounding landscape.

PAs also have the potential to be important for species that they were not designated for, if they become climatically suitable for these new species. A wide range of southerly-distributed, warm-adapted species disproportionately colonise PAs compared with the surrounding landscape (Thomas *et al.* 2012), with some species achieving higher abundances on PAs compared with non-PA sites in colonised areas (Gillingham *et al.* 2014). In addition, six species of wetland birds that have recently colonised the UK naturally from other areas of Europe have used PAs to facilitate their expansion (Hiley *et al.* 2013). However, it is not clear whether this apparent reliance on PAs during expansion is due to the protection afforded by designation, or because PAs in Great Britain tend to be located at higher latitudes and altitudes than unprotected land, since these are the places most likely to be colonised as the climate improves for expanding species.

Here, we examine empirical evidence obtained from detailed resurveys of 7 species of butterfly (4 northern and 3 southern) and 11 birds (six northern and five southern). We use these high quality data to determine whether PAs have retained species that have undergone local extinctions at their warm range margins in recent years. We also determine whether species are reliant on PAs when colonising new locations, or whether the apparent reliance on PAs is a result of the disproportionate protection within Great Britain of land at higher altitudes and latitudes.

Material and Methods

Data sources and re-surveys of butterflies and birds

We used extensive atlas data (Asher *et al*. 2001) to determine historic presence along with survey data from Franco *et al.* (2006) for four butterfly species with northern distributions in Great Britain. For three butterflies with southern distributions in Great Britain, detailed resurvey data were available (Thomas *et al.,* 2001, Thomas, Simcox & Clarke, 2009, Wilson, Davies & Thomas, 2009, Bennie *et al.,* 2013). We used data from the Statutory Conservation Agency/RSPB Annual Breeding Bird Scheme (SCARABBS) database (available at https://data.nbn.org.uk/) for five birds with southern distributions in Great Britain and six birds with northern distributions in Great Britain (see Table 1 for species included), supplemented with National Atlas data (Gibbons, Reid & Chapman 1993).

These were the only species with northern or southern range margins lying within Great Britain with comprehensive resurvey data available at a national scale. The surveys cover the whole extent of each species' range and are not biased towards surveying PAs over non-PA land. For each site visited during the resurveys, it was noted whether the focal species was present or absent. The resurveys therefore allow deduction of species persistence, colonisation or local extinction. However, in contrast to the high quality resurvey datasets, there was a lack of information on absences from many of the earlier surveys, and so sites outside the species' known range at that time were not included as definite absences. Nonetheless, for the birds included here the first time period (termed time period 1, see below) coincides with the publication of an atlas and hence 10 km squares without a presence could probably be regarded as true absences.

We defined PAs as Sites of Special Scientific Interest (SSSIs) as this corresponds to level IV IUCN protection and forms the basis for other designations in Great Britain with biodiversity conservation as the primary objective. We used shapefiles of SSSI extent provided by Natural England, Natural Resources Wales and Scottish Natural Heritage and calculated the percentage of each 1 km^2 grid square that fell within a SSSI.

Determining distribution changes

After collating all available data for the study species, 1 km^2 grid squares were assigned as "extinct", "persisted", "colonised" or "uncolonised" for each study species as follows. First , we considered the extent of occurrence for each study species in the first time period (T1, see table 1) to be all 10 x 10 km squares (i.e. hectads, subsequently termed '10 km grid squares') with presence records in this time period. Next, we considered 1 km^2 grid squares to be 'colonised' by a species if there was a record from the later time period (T2, see table 1) located outside this T1 extent of occurrence. In addition, we designated 1 km^2 squares that were unoccupied in T2 but were within a 10 km grid square with at least one record of colonisation by that species as 'uncolonised'. This assumes that the species was not present in these locations in T1, but that it could have colonised these locations during T2, given their close proximity. This assumption was necessary because surveys in T1 were only carried out in species' current range at that time, with no data to confirm historical absences in the colonising range. Squares were designated as ‘persisted’ if the 1 km^2 square was occupied in both T1 and in T2. Squares were considered to be ‘extinct’ if the 1 km^2 square was occupied in T1 and was visited but the species was not found in T2 after a comparable search effort.

Statistical Analysis

For the northern species, generalised linear models (glms) were fitted to extinct (0) and persisted (1) locations using a binomial error structure and logit-link function. To account for latitudinal and altitudinal shifts in species’ distributions (e.g. Hickling *et al.* 2006, Chen *et al.* 2011), we included the average latitude (in Km north of the false origin of the British National Grid) and elevation (in metres above sea level) of each 1 km^2 square as explanatory variables, in addition to the percentage of each 1 km^2 square that was considered to be within a PA. For the southern species, glms were fitted to uncolonised (0) and colonised (1) locations with the same independent variables. Because this resulted in a large number of uncolonised records, we repeated these analyses with a random subset of ‘uncolonised’ records of equal number to the number of colonised records available (see table S1). To account for the number of tests completed out, we carried out Bonferroni corrections to show which results remain significant. Finally, to test the generality of our results, we fitted GLMMs with the same dependent and independent variables as above plus the inclusion of interactions between latitude and altitude, latitude and PA and altitude and PA (note that there was not enough statistical power to fit these interaction terms for all species individually) with species identity as a random factor, in the R package lme4 (Bates *et al.* 2014). These were fitted (a) for all southern and northern species, and (b) separately for northern and southern birds and butterflies, to allow comparison between taxa. All spatial analyses were carried out in ArcMap v.10 and all statistical analyses were performed in R version 3.1.1 (R Core Team 2014).

Results

Northern species

Of the ten northern species, which all had records of extinction (Table 2), two showed a significant positive relationship between persistence and latitude ($p<0.001$, Northern Brown Argus and Scotch Argus), meaning that these species were more likely to survive at more northerly locations. Two species showed a significant positive relationship between survival and altitude ($p<0.05$, Mountain Ringlet and Black Grouse), although only the Mountain Ringlet remained significant after the application of Bonferroni corrections, meaning that this species was more likely to persist at higher altitudes. One species showed a significant negative relationship with altitude (Slavonian Grebe, $p<0.05$, although this relationship did not remain significant after Bonferroni corrections). No northern species showed a significant positive relationship with % PA cover (although Black Grouse and Woodlark were significant before Bonferroni corrections) suggesting that PA status had little impact on species' survival at their trailing edge range margins.

Whether considering all northern species together, or birds and butterflies separately, with the inclusion of interaction terms, % PA cover was a positive predictor of survival in the mixed effects model (Table 3). There was also a significant positive effect of both latitude and altitude on survival across all northern species. When considering the two taxonomic groups separately, only latitude showed a significant positive effect, which was present for both groups. The significantly negative interaction terms between PA and altitude (for all northern species together) and PA and latitude (in all northern analyses) mean that the positive effect of PA on persistence was higher at lower altitudes and latitudes, whilst the positive effects of increasing altitude and latitude were lower at higher coverages of PA. Thus, in contrast to our single species analyses, we found evidence for PA status affecting persistence of northern species, but only at lower altitudes and latitudes.

Southern species with records of colonisation

Of the eight southern species with sufficient data to investigate colonisation patterns (Table 2), six showed a significant positive relationship with PA coverage (five after Bonferroni corrections), such that colonised squares had a higher proportion of protected land than those that were not colonised. In contrast, for the Nightjar the relationship with PA coverage was significantly negative at $p<0.05$, such that uncolonised locations had a higher coverage of PA than those that were colonised. However, this relationship did not remain significant after Bonferroni corrections were applied. In addition, the colonisations of five (four after Bonferroni corrections) southern species were at significantly higher altitudes than uncolonised sites. Although Bittern was found to colonise significantly lower altitude sites, this did not remain significant after Bonferroni corrections. Colonisations were sometimes at lower latitudes than uncolonised sites; three species showed a significant negative relationship at $p<0.05$, although only the Silver-spotted Skipper remained significant after Bonferroni corrections. Thus in contrast to northern species when analyses individually, PA status was important for colonisation success in most (five out of eight) of our study species.

When considering all southern species together, PA coverage was a significant positive predictor of colonisation (Table 3). This effect remained significant for southern birds. In addition, for all southern species together, and for southern birds separately, there was a significant positive effect of altitude, such that colonisations occurred in squares at higher altitudes, and latitude, such that colonisations occurred in more northerly locations. There was a significant negative interaction between altitude and latitude when considering all southern species together, as well as for the southern birds, such that the positive effect of altitude is less at higher latitudes. For these two analyses there were also significant negative interactions between PA and latitude and PA and altitude, such that the positive effect of PA coverage was stronger at lower altitudes and latitudes. For southern butterflies the picture appears to be somewhat different, with a significant negative effect of latitude on colonisation probability and a significantly positive interaction between PA coverage and altitude.

Discussion

When looking across species, we found evidence to suggest that PAs help to retain species undergoing local extinctions within Great Britain. The finding that the positive effects of PA coverage are lower at higher elevations and latitudes are perhaps not surprising, given that populations located further south and at lower altitudes will have experienced higher levels of stress due to climatic change. However, when species were analysed individually, only one (Black Grouse) of ten northern species showed a significant positive relationship between % PA coverage and persistence, and the result for this species was not significant after the application of Bonferroni corrections. This species has been the subject of an extensive management programme (Grant *et al.* 2009) which may have had some success, although some initiatives have also taken place outside PAs which may explain the lack of a strong effect of PA status in our analyses. The lack of evidence for an effect of PAs in retaining northern species in the individual species analyses may also have been due to the lack of power to allow inclusion of interaction terms rather than a lack of effect. However, it agrees somewhat with the findings of Virkkala *et al.* (2014), who showed that for the majority of 90 Finnish birds of conservation concern, trends in species richness between 1974-89 and 2000-2006 were the same on and off PAs (although for birds preferring mires, species richness decreased less in PAs than outside them) - PAs maintained higher species richness than the surrounding areas, but there was no extra effect of protection for most species.

The potential for PAs to help protect species from deteriorating climates remains worthy of further investigation. There is evidence for some upland bird species threatened by climate change that specific management may increase their ability to persist in an increasingly unfavourable climate (Pearce-Higgins *et al.* 2011, Carroll *et al.* 2011), and more work is required to test the generality of this finding. Because not all SSSIs are under active management, effectiveness of PA management could not be determined here. More detailed data on the impacts of management regimes, comparing managed areas to unmanaged locations, would help to determine if this is an option in future, at least for those species that are unable to disperse to newly suitable areas. Moreover, past management has not generally been designed with climatic change in mind, and future management that is designed specifically to minimise the impacts of climatic change on features of interest may meet with more success. For example, increasing habitat heterogeneity at sites may increase population stability and hence prevent extinctions (Oliver *et al.* 2014). Finally, although not specifically investigating climatic change, Donald *et al.* (2007) discovered a positive effect of the percentage of a country designated as a Special Protection Area under the Birds Directive on the population trends of Annexe 1 species in Europe, suggesting that managed PAs can increase the population sizes of target species.

Colonised 1 km^2 locations had higher PA coverage than locations that remained uncolonised for five out of eight of our study species when modelled individually, as well as in the combined taxon analysis, reinforcing our growing understanding that PA designation can be important in determining the suitability of a location for colonisation during range expansion. This agrees with the findings of Beale *et al.* (2013), Thomas *et al.* (2012) and Hiley *et al.* (2013). The additional inclusion of latitude and altitude as independent variables in our study shows that this effect was not simply due the location of PAs at higher altitudes and latitudes within Great Britain, the locations that would become more suitable during climatic change. The positive effect of PA designation on colonisation may be due to a lack of suitable habitat outside PAs, rather than active management or protection in PAs *per se* (see Pearce-Higgins & Green, 2014), although informed management has been demonstrably important in the recovery since 1990 of the three southern butterfly species studied here (Lawson *et al.* 2014a; Thomas, Hovestadt & Simcox 2011; O'Connor, Hails & Thomas 2014). We were unable to differentiate uncolonised and colonised sites within the core extent of occurrence (i.e. range infilling), where these recoveries have taken place. Routine recording of absences in future would increase the power of analyses such as those presented here.

Our analyses also reinforce the general conclusion that many species have changed their British distributions in the direction expected if they were responding to climatic change: many species have colonised or persisted better at higher latitudes and altitudes. The effects of altitude and latitude are stronger, in terms of number of species responding, at the expanding edge of species' ranges than at the trailing edge of current ranges. However, there was one exception, the Silver-spotted Skipper butterfly, which colonised lower latitudes. The result for this species also probably drove the significant negative effect of latitude in the mixed effect model for southern butterflies (over half the records included were of Silver-spotted Skipper). This may be due to more rapid infilling of the southernmost part of its British distribution (where more empty habitat was available) than extension northwards (where habitat is highly fragmented). There is also the interplay between latitude and altitude to consider: Lawson *et al.* (2014b) recently showed that temperatures experienced by the Silver-spotted Skipper during its flight period depended more on topographic heterogeneity within 5 km grid cells than climatic difference between them. Although the negative effect of latitude on colonisation of southern butterflies remained significant in the mixed effects model despite the inclusion of an interaction between latitude and altitude, we conclude that this effect is driven primary by the Silver-spotted Skipper having a disproportionate effect.

Generally, more significant results were obtained for southern than for northern species in the individual species analyses. It is possible that this is an artefact at least in part of the larger number of recorded locations for individual southern species. However, the models with equal numbers of colonised and uncolonised species (See Tables S1 and S2) show that these significant results are not solely down to the number of records included.

We do not endorse the view that PA status should be removed if feature species are lost, i.e. the reserve might be considered to have ‘underperfomed’ (e.g. Fuller *et al*. 2010). Some reserves protect areas with a unique combination of geophysical factors, which have been posited as drivers of regional species richness (Anderson & Ferree 2010). In addition, we found some evidence that PAs retain species undergoing retractions at their warm range margins. Although individual PAs may lose some of the features for which they are currently designated due to climatic change (e.g. Araújo *et al.* 2011, Hole *et al.* 2009), species that are expanding their cold range boundaries polewards do move into these areas and many of these species are also of conservation concern (Thomas *et al.* 2012, Beale *et al.* 2013, Hiley *et al.* 2013, this study). Hence PAs may gain species of conservation value as fast or faster than they lose them (Johnston *et al.* 2013), which should be taken into account when assessing their likely future effectiveness (e.g. Leach, Zalat & Gilbert, 2013). In heavily human-modified countries such as England, PAs represent the majority of suitable semi-natural locations that could be colonised (Lawton *et al.* 2010) and degazettement following loss of feature species could result in an overall reduction in the area of semi-natural vegetation due to conversion to other uses. In future, PAs may continue to support important populations of rare and threatened species simply because they protect vulnerable natural and semi-natural habitats from inputs of nutrients and pesticides as well as conversion to other land cover types, even if the precise species composition at a site differs from that currently found there (Johnston *et al.* 2013). Reserve managers in Great Britain already monitor and manage habitats for some species that they were not designated for (Davies *et al.,* 2007) and there is some evidence that active management aids the colonisation of PAs by species expanding their distributions (Lawson *et al.,* 2014a) as well as the possibility that management might aid retention of contracting species (Pearce-Higgins 2011). We suggest that PA management should be designed with climatic change in mind, and effective monitoring systems should be implemented to test the effects of this management.

Acknowledgements

We thank the many recorders responsible for data collection. We thank the Biological Records Centre, British Trust for Ornithology, Butterfly Conservation, Natural Resources

Wales (formerly Countryside Council for Wales), Forestry Commission, Joint Nature Conservation Committee, Natural England, Natural Environment Research Council, Royal Society for the Protection of Birds, and Scottish Natural Heritage for data and/or financial support for surveys. The project was funded by a KE Grant from NERC.

References

Anderson MG, Ferree CE. 2010. Conserving the stage: Climatic change and the geophysical underpinnings of species diversity. *Public Library of Sciences One* **5:** e11554.

Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W. 2011. Climatic change threatens European conservation areas. *Ecology Letters* **14:** 484-492.

Araújo MB, Cabeza M, Thuiller W, Hannah L, Williams PH. 2004. Would climatic change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology* **10:** 1618-1626.

Asher J, Warren M, Fox R, Harding P, Jeffcoate G, Jeffcoate S. 2001. *Millenium atlas of butterflies in Britain and Ireland.* Oxford University Press, Oxford, UK.

Bagchi R, Crosby M, Huntley B, Hole DG, Butchart SH, Collingham Y, Kalra M, Rajkumar J, Rahmani A, Pandey M, Gurung H, Trai L, Van Quang N, Willis SG. 2013. Evaluating the effectiveness of conservation site networks under climatic change: accounting for uncertainty. *Global Change Biology* **19:** 1236-1248.

Bates D, Maechler M, Bolker B, Walker S. 2014. *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7

Beale CM, Baker NE, Brewer MJ, Lennon JJ. 2013. Protected area networks and savannah bird biodiversity in the face of climatic change and land degradation. *Ecology Letters* **16:** 1061-1068.

Bennie J, Hodgson JA, Lawson CR, Holloway CTR, Roy DB, Brereton T, Thomas CD, Wilson RJ. 2013. Range expansion through fragmented landscapes under a variable climate. *Ecology Letters* **16:** 921-929.

Carroll MJ, Dennis P, Pearce-Higgins JW & Thomas CD. 2011. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. *Global Change Biology* **17:** 2991-3001.

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333:** 1024-1026.

Davies H, Brereton TM, Roy DB, Fox R. 2007. Government targets for protected area management: will threatened butterflies benefit? *Biodiversity Conservation* **16:** 3719-3736.

Donald PF, Sanderson FJ, Burfield IJ, Bierman SM, Gregory RD, Waliczky Z. 2007. International conservation delivers benefits for birds in Europe. *Science* **317**: 810–813.

Franco AF, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B, Thomas CD. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* **12:** 1545-1553.

Fuller RA, McDonald-Madden E, Wilson KA, Carwardine J, Grantham HS, Watson JEM, Klein CJ, Green DC, Possingham HP. 2010. Replacing underperforming protected areas achieves better conservation outcomes. *Nature* **466:** 365-367.

Gibbons DW, Reid JB, Chapman RA. 1993. *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. T. & A.D. Poyser, London

Gillingham PK, Alison J, Roy DB, Fox R, Thomas CD. 2014. High abundances of species in protected areas in parts of their geographic distributions colonized during a recent period of climatic change. *Conservation Letters* early online

Gillingham PK. 2013. *Implications of climatic change for SSSIs and other protected areas.* Terrestrial biodiversity climatic change impacts report card technical paper 4, Living With Environmental Change, UK.

Grant MC, Cowie N, Donald C, Dugan D, Johnstone I, Lindley P, Moncreiff R, Pearce-Higgins JW, Thorpe R, Tomes D. 2009. Black grouse response to dedicated conservation management. *Folia Zoologica* **58:** 195-206.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12:** 450-455.

Hiley JR, Bradbury RB, Holling M, Thomas CD. 2013. Protected areas act as establishment centres for species colonising the UK. *Proceedings of the Royal Society B* **280**: 20122310.

Hole DG, Willis SG, Pain DJ, Fishpool LD, Butchart SH, Collingham YC, Rahbek C, Huntley B. 2009. Projected impacts of climatic change on a continent-wide protected area network. *Ecology Letters* **12**: 420-431.

**Johnston A, Ausden M, Dodd AM, Bradbury RB, Chamberlain DE, Jiguet F, Thomas CD, Cook ASCP, Newson SE, Ockendon N, Rehfisch MM, Roos S, Thaxter CB, Brown A, Crick HQP, Douse A, McCall RA, Pontier H, Stroud DA, Cadiou B, Crowe O, Deceuninck B,

Hornman M, Pearce-Higgins JW. 2013. Observed and predicted effects of climatic change on species abundance in protected areas. *Nature Climate change* **3**: 1055-1061.

Kharouba HM, Kerr JT. 2010. Just passing through: Global change and the conservation of biodiversity in protected areas. *Biological Conservation* **143**: 1094-1101.

Lawson CR, Bennie J, Hodgson JA, Thomas CD, Wilson RJ. 2014b. Topographic microclimates drive microhabitat associations at the range margin of a butterfly. *Ecography* **37**: 732-740.

Lawson CR, Bennie JJ, Thomas CD, Hodgson JA, Wilson RJ. 2014a. Active management of protected areas enhances metapopulation expansion under climatic change. *Conservation Letters* **7**: 111-118.

Lawton JH, Brotherton PNM, Brown VK, Elphick C, Fitter AH, Forshaw J, Haddow RW, Hilborne S, Leafe RN, Mace GM, Southgate MP, Sutherland WA, Tew TE, Varley J, Wynne, GR. 2010. *Making Space for Nature: a review of England's wildlife sites and ecological network*. Report to Defra.

Leach K, Zalat S, Gilbert F. 2013. Egypt's protected area network under future climatic change. *Biological Conservation* **159:** 490-500.

Mair L, Thomas CD, Anderson BJ, Fox R, Botham M, Hill JK. 2012. Temporal variation in responses of species to four decades of climate warming. *Global Change Biology* **18:** 2439-2447.

Mascia M, Pailler S. 2011. Protected area downgrading, downsizing and degazettement (PADDD) and its conservation implications. *Conservation Letters* **4:** 9-20.

O'Connor RS, Hails RS, Thomas JA. 2014. Accounting for habitat when considering climate: has the niche of the Adonis blue butterfly changed in the UK? *Oecologia* **174**: 1463-1472.

Oliver TH, Stefanescu C, Páramo F, Brereton T, Roy DB. 2014. Latitudinal gradients in butterfly population variability are influenced by landscape heterogeneity. *Ecography* **37**: 863-871.

Pearce-Higgins W, Green RE. 2014. *Birds and climate change: Impacts and conservation responses.* Cambridge University Press

Pearce-Higgins JW. 2011. Modelling conservation management options for a southern range-margin population of Golden Plover *Pluvialis apricaria* vulnerable to climatic change. *Ibis* **153**: 345-356.

Peters RL, Darling JDS. 1985. The greenhouse-effect and nature reserves. *Bioscience* **35:** 707–717.

R Core Team. 2014. *R: A language and environment for statistical computing*. R foundation for statistical computing, Vienna, Austria. URL http://www.R-project.org/.

Rayfield B, James PMA, Fall A, Fortin M-J. 2008. Comparing static versus dynamic protected areas in the Québec boreal forest. *Biological Conservation* **141**: 438-449.

Thomas CD, Gillingham PK, Bradbury RB, Roy DB, Anderson BJ, Baxter JM, Bourn NAD, Crick HQP, Findon RA, Fox R, Hodgson JA, Holt AR, Morecroft MD, O'Hanlon NJ, Oliver TH, Pearce-Higgins JW, Procter DA, Thomas A, Walker KJ, Walmsley CA, Wilson RJ, Hill JK. 2012. Protected areas facilitate species range expansions. *Proceedings of the National Academy of Sciences USA* **109:** 14063-14068.

Thomas JA, Simcox DJ, Hovestadt T. 2011. Evidence based conservation of butterflies. *Journal of Insect Conservation* **15:** 241-258.

Thomas JA, Simcox DJ, Clarke RT. 2009. Successful conservation of a threatened Maculinea butterfly. *Science* **325:** 80–83.

Thomas JA, Bourn NAD, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R, Goodger B. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes*. Proceedings of the Royal Society of London B: Biological Sciences* **268**: 1791-1796.

Virkkala R, Pöyry J, Heikkinen RK, Lehikoinen A, Valkama J. 2014. Protected areas alleviate climatic change effects on northern bird species of conservation concern. *Ecology and Evolution* early online, doi: 10.1002/ece3.1162

Wilson RJ, Davies ZG, Thomas CD. 2009. Modelling the effect of habitat fragmentation on range expansion in a butterfly. *Proceedings of the Royal Society of London B: Biological Sciences* **276:** 1421-1427.

Zografou K, Kati V, Grill A, Wilson RJ, Tzirkalli E, Pamperos LN, Halley JM. 2014. Signals of climatic change in butterfly communities in a Mediterranean protected area. *Public Library of Sciences One* **9**: e87245.

Figure 1: The mean percentage cover of PA in 1 km^2 grid squares for each species a) with records of colonisation (grey bars) or that were uncolonised (white bars) and b) with records of persistence (grey bars) or where the species went extinct (white bars). Presented also are the standard errors of the mean, analyses that were significant at $p < 0.05$ are marked with *, $p < 0.001$ with ***

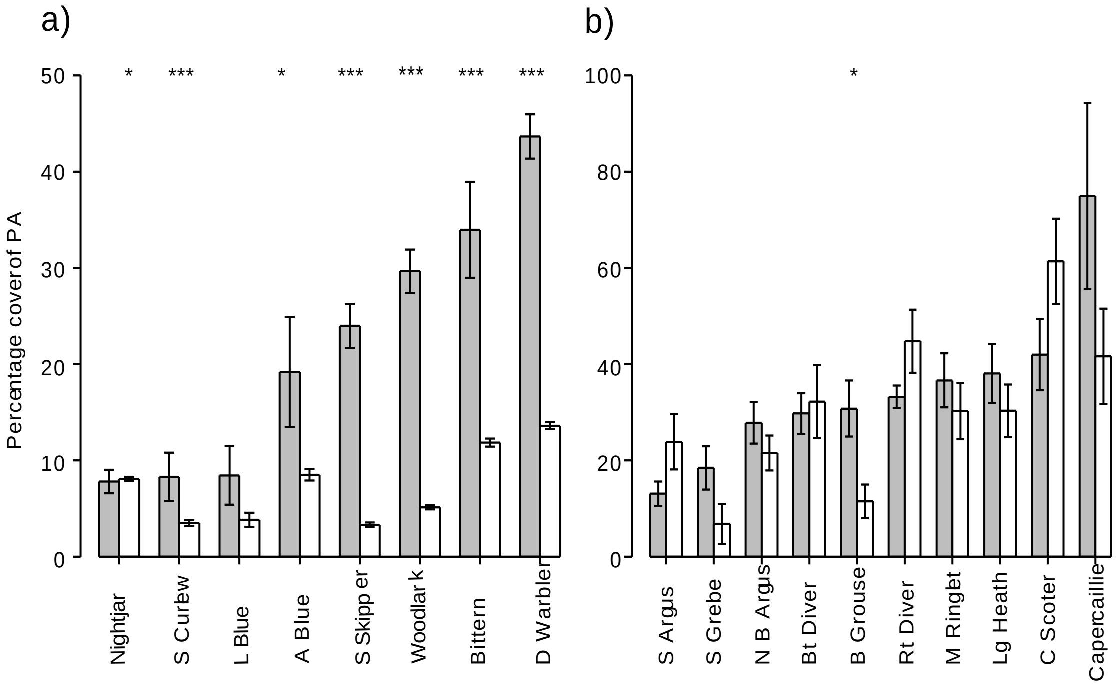

Table 1: Study species with sufficient data for analysis. N denotes species with a northern distribution within Great Britain, S denotes species with a southern distribution in Great Britain. T1 refers to the first time period analysed, T2 to the second time period analysed. Presented here are the number of 1 km2 locations that were classified as either E (extinct), S (survived), C (Colonised) and U (Uncolonised). A dash – indicates not investigated.

Taxon	Species	Distribution	T1	T2	E	S	C	U
Butterfly	Large Heath *Coenonympha tullia*	N	1970-82, 1995-99	2004-05	55	42	-	-
Butterfly	Mountain Ringlet *Erebia epiphron*	N	1970-82, 1995-99	2004-05	41	57	-	-
Butterfly	Northern Brown Argus *Aricia artaxerxes*	N	1970-82, 1995-99	2004-05	62	58	-	-
Butterfly	Scotch Argus *Erebia aethiops*	N	1970-82, 1995-99	2004-05	35	112	-	-
Bird	Black Grouse *Tetrao tetrix*	N	1995-96	2005	54	42	-	-
Bird	Black-throated Diver *Gavia arctica*	N	1994	2006	26	90	-	-
Bird	Capercaillie *Tetrao urogallus*	N	1992-94	2010	17	5	-	-
Bird	Common Scoter *Melanitta nigra*	N	1995	2007	20	30	-	-
Bird	Red-throated Diver *Gavia stellata*	N	1994	2006	51	325	-	-
Bird	Slavonian Grebe *Podiceps auritus*	N	1970s	2000s	24	27	-	-
Butterfly	Adonis Blue *Polyommatus bellargus*	S	1978	1997, 1999	-	29	16	1181
Butterfly	Large Blue *Maculinea arion*	S	1992	2008	-	4	11	385
Butterfly	Silver-spotted Skipper *Hesperia comma*	S	1982, 1991	2000, 2009	-	30	105	2090
Bird	Bittern *Botaurus stellaris*	S	1990-91	1992-2008	-	12	49	3702
Bird	Dartford Warbler *Sylvia undata*	S	1974, 1984	1994, 2006	-	223	230	6265
Bird	Nightjar *Caprimulgus europaeus*	S	1980-82	1994, 2004-05	-	352	240	11553
Bird	Stone Curlew *Burhinus oedicnemus*	S	1985-91	1992-2010	-	200	84	1810
Bird	Woodlark *Lullula arborea*	S	1986	2006	-	110	245	6475

Table 2: GLM results for species with records of extinction (Analysis code E) and colonisation (Analysis code C). For each explanatory variable (PA: Percentage of Protected Area, Altitude: Mean altitude of 1 km^2 grid square, Latitude: Y co-ordinate of centre of 1 km^2 grid square in Km), we give the coefficient of the relationship and the standard error of the coefficient in brackets, along with the p-value associated with each. Values in bold font are significant after the application of Bonferroni corrections.

Species	Analysis	PA		Altitude		Latitude	
		Coeff (S.E.)	p	Coeff (S.E.)	p	Coeff (S.E.)	p
Large Heath *Coenonympha tullia*	E	0.0052 (0.0052)	0.3150	-0.0009 (0.0014)	0.4960	0.0011 (0.0014)	0.4360
Mountain Ringlet *Erebia epiphron*	E	-0.0046 (0.0060)	0.4407	**0.0059** **(0.0017)**	**0.0006**	0.0018 (0.0021)	0.3702
Northern Brown Argus *Aricia artaxerxes*	E	0.0127 (0.0067)	0.0590	-0.0015 (0.0017)	0.3785	**0.0056** **(0.0016)**	**0.0006**
Scotch Argus *Erebia aethiops*	E	-0.0112 (0.0067)	0.0972	0.0012 (0.0019)	0.5418	**0.0072** **(0.0020)**	**0.0002**
Black Grouse *Tetrao tetrix*	E	0.0165 (0.0076)	0.0308	0.0068 (0.0030)	0.0230	0.0030 (0.0016)	0.0610
Black-throated Diver *Gavia arctica*	E	-0.0008 (0.0057)	0.8900	-0.0011 (0.0022)	0.6090	-0.0017 (0.0031)	0.5850
Capercaillie *Tetrao urogallus*	E	0.0107 (0.0120)	0.3720	-0.0434 (0.0072)	0.5450	-0.0522 (0.0390)	0.1810
Common Scoter *Melanitta nigra*	E	-0.0089 (0.0079)	0.2590	-0.00003 (0.0022)	0.9880	-0.0033 (0.0041)	0.4260
Red-throated Diver *Gavia stellata*	E	-0.0045 (0.0037)	0.2200	-0.0020 (0.0022)	0.3490	0.0005 (0.002)	0.7820
Slavonian Grebe *Podiceps auritus*	E	0.0209 (0.0151)	0.1649	-0.0080 (0.0039)	0.0432	-0.0417 (0.0326)	0.2016
Bittern *Botaurus stellaris*	C	**0.0167** **(0.0038)**	**<0.0001**	-0.0193 (0.0085)	0.0220	0.0019 (0.0014)	0.1560
Dartford Warbler *Sylvia undata*	C	**0.0221** **(0.0017)**	**<0.0001**	0.0004 (0.0005)	0.4590	-0.0016 (0.0011)	0.1350
Nightjar *Caprimulgus europaeus*	C	-0.0074 (0.0032)	0.0202	**0.0028** **(0.0005)**	**<0.0001**	-0.0011 (0.0004)	0.0048
Stone Curlew *Burhinus oedicnemus*	C	**0.0199** **(0.0056)**	**0.0004**	**0.0144** **(0.0022)**	**<0.0001**	0.0054 (0.0020)	0.0078
Woodlark *Lullula arborea*	C	**0.0310** **(0.0019)**	**<0.0001**	0.0024 (0.0010)	0.0208	-0.0005 (0.0006)	0.3757
Adonis Blue *Polyommatus bellargus*	C	0.0241 (0.0094)	0.0104	**0.0175** **(0.0050)**	**0.0005**	-0.0554 (0.0251)	0.0277
Large Blue *Maculinea arion*	C	0.0202 (0.0148)	0.1730	0.0200 (0.0124)	0.1070	0.0376 (0.0585)	0.5200
Silver-spotted Skipper *Hesperia comma*	C	**0.0512** **(0.0047)**	**<0.0001**	**0.0126** **(0.0022)**	**<0.0001**	**-0.0231** **(0.0040)**	**<0.0001**

Table 3: Results from the Mixed Effects models. N is the number of 1 km^2 locations included. For each explanatory variable (PA: Percentage of Protected Area, Altitude: Mean altitude of 1 km^2 grid square, Latitude: Y co-ordinate of centre of 1 km^2 grid square in Km) we give the coefficient of the relationship and the standard error of the coefficient in brackets, along with the p-value associated with each. Values in bold font are significant at $p < 0.05$.

Group	N	PA	p	Altitude	p	Latitude	p	Altitude * Latitude	p	PA*Latitude	p	PA*Altitude	p
Northern Butterflies	462	**0.0443** **(0.0148)**	**0.0028**	0.0017 (0.0032)	0.6015	**0.0049** **(0.0014)**	**0.0004**	0.0000004 (0.000004)	0.9227	**-0.000049** **(0.0000021)**	**0.0184**	-0.000025 (0.000013)	0.0599
Northern Birds	711	**0.0549** **(0.0188)**	**0.0035**	0.0048 (0.0033)	0.1462	**0.0033** **(0.0015)**	**0.0221**	-0.00004 (0.000004)	0.2602	**-0.000050** **(0.000016)**	**0.0018**	-0.000042 (0.000024)	0.0804
Northern Species	1173	**0.0428** **(0.0096)**	**<0.0001**	**0.0052** **(0.0020)**	**0.0105**	**0.0044** **(0.0008)**	**<0.0001**	-0.000004 (0.000003)	0.1279	**-0.000040** **(0.000009)**	**<0.0001**	**-0.000033** **(0.000011)**	**0.0022**
Southern Butterflies	3788	0.0087 (0.0162)	0.5918	0.0069 (0.0075)	0.3519	**-0.0287** **(0.0084)**	**0.0007**	0.000016 (0.000056)	0.7699	0.000143 (0.000143)	0.3152	**0.000214** **(0.000070)**	**0.0021**
Southern Birds	30645	**0.0340** **(0.0022)**	**<0.0001**	**0.0060** **(0.0006)**	**<0.0001**	**0.0010** **(0.0004)**	**0.0211**	**-0.000008** **(0.000002)**	**<0.0001**	**-0.000023** **(0.000008)**	**0.0046**	**-0.000071** **(0.000006)**	**<0.0001**
Southern Species	34433	**0.0354** **(0.0021)**	**<0.0001**	**0.0061** **(0.0006)**	**0.0002**	**0.0009** **(0.0004)**	**0.0268**	**-0.000009** **(0.000002)**	**<0.0001**	**-0.000025** **(0.000008)**	**0.0016**	**-0.000072** **(0.000006)**	**<0.0001**