The Linnean Society of London — BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2015, **115**, 707–717. With 1 figure.

The effectiveness of protected areas in the conservation of species with changing geographical ranges

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Received 7 November 2014; revised 12 January 2015; accepted for publication 12 January 2015

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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 that they were designated to protect, and may not be located appropriately to receive newly-colonizing species for which the climate is improving. In the present study, we analyze fine-scale distribution data from detailed resurveys of seven butterfly and 11 bird species in Great Britain aiming to examine any effect of PA designation in preventing extinctions and promoting colonizations. We found a positive effect of PA designation on species' persistence at trailing-edge warm range margins, although with a decreased magnitude at higher latitudes and altitudes. In addition, colonizations by range expanding species were more likely to occur on PAs even after altitude and latitude were 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.

ADDITIONAL KEYWORDS: adaptation – birds – butterflies – climate change – colonization – conservation – extinction – reserves – site of special scientific interest – SSSI.

INTRODUCTION

We now have strong evidence indicating that a wide range of species are changing their distributions in response to recent climatic change (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 them, and other species contracting from areas where the climate has become less suitable (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 others will experience a high turnover of species in the future (Hole *et al*., 2009; Bagchi *et al*., 2013). Some studies 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, because species respond individualistically to the same level of environmental change (Mair *et al*., 2012) and, in countries with a high human pressure such as England, there is not very much natural or semi-natural habitat to be found outside current protected areas (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 facilitate persistence under climatic change.

PAs also have the potential to be important for species that they were not designated for, especially if they become climatically suitable for these new species. A wide range of southerly-distributed, warm-adapted species disproportionately colonize PAs compared to the surrounding landscape (Thomas *et al*., 2012), with some species achieving higher abundances on PAs compared to non-PA sites in colonized areas (Gillingham *et al*., 2015). In addition, six species of wetland birds that have recently colonized 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 a result of the protection afforded by designation, or because PAs in Great Britain tend to be located at higher latitudes and altitudes than unprotected land because these are the places most likely to be colonized as the climate improves for expanding species (Gillingham, 2013).

In the present study, we examine empirical evidence obtained from detailed resurveys of seven species of butterfly (four northern and three 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 colonizing 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 (https://data.nbn.org.uk/) for five birds with southern distributions in Great Britain and six birds with northern distributions in Great Britain (for species included, see Table 1),

Table 1. Study species with sufficient data for analysis

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

N, species with a northern distribution within Great Britain; S, species with a southern distribution in Great Britain. T1, first time period analyzed; T2, second time period analyzed. The number of 1-km^2 locations that were classified as either E (extinct), S (survived), C (Colonized), and U (Uncolonized) is also shown. –, not investigated.

supplemented with National Atlas data (Gibbons, Reid & Chapman, 1993).

Birds and butterflies are the best recorded taxonomic groups within Great Britain, and these were the only species of any taxonomic group 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, colonization 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 in the present study, the first time period (termed time period 1; see below) coincides with the publication of an atlas and hence 10-km^2 squares without a presence were assumed to reflect true absences.

We defined PAs as Sites of Special Scientific Interest (SSSIs) because this corresponds to level IV IUCN (International Union for Conservation of Nature) 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 the available data for the study species, 1-km^2 grid squares were assigned as 'extinct', 'persisted', 'colonized' or 'uncolonized' for each study species. First, we considered the extent of occurrence for each study species in the first time period (T1) (Table 1) to be all 10 × 10 km squares (i.e. hectads, subsequently termed '10-km^2 grid squares') with presence records in this time period. Next, we considered 1-km^2 grid squares to be 'colonized' by a species if there was a record from the later time period (T2) (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^2 grid square with at least one record of colonization by that species as 'uncolonized'. This assumes that the species was not present in these locations in T1 but that it could have colonized 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 colonizing 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, generalized linear models (GLMs) were fitted to extinct (0) and persisted (1) locations using a binomial error structure and logit-link function (analysis code E) (Table 2). To account for latitudinal and altitudinal shifts in species' distributions (Hickling *et al*., 2006; Chen *et al*., 2011), we included the mean latitude (km north of the false origin of the British National Grid) and elevation (m.a.s.l.) 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 uncolonized (0) and colonized (1) locations with the same independent variables (analysis code C) (Table 2). Because this resulted in a large number of uncolonized records, we repeated these analyses with a random subset of 'uncolonized' records of equal number to the number of colonized records available (see Supporting information, Table S1). To account for the number of tests completed, we carried out Bonferroni corrections. Finally, to test the generality of our results, we fitted generalized linear mixed models (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 (1) for all southern and northern species and (2) separately for northern and southern birds and butterflies, allowing comparison between taxa. All spatial analyses were carried out in ARCMAP, version 10 (ESRI) 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

Table 2. Generalized linear model results for species with records of extinction (analysis code E) and colonization (analysis code C)

		PA		Altitude		Latitude	
Species	Analysis	Coefficient (± SE)	*P*	Coefficient (± SE)	*P*	Coefficient (± SE)	*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 ± 0.0020	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**

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 parenthesis, along with the *P*-value associated with each. Values shown in bold are significant after the application of Bonferroni corrections.

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 percentage PA cover (although black grouse and woodlark were significant before Bonferroni corrections; Fig. 1), 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, percentage 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, whereas 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, although only at lower altitudes and latitudes.

Southern species with records of colonization

Of the eight southern species with sufficient data to investigate colonization patterns (Table 2), six showed a significant positive relationship with PA coverage (five after Bonferroni corrections; Fig. 1), such that colonized squares had a higher proportion of protected land than those that were not colonized. By contrast, for the nightjar, the relationship with PA coverage was significantly negative at $P < 0.05$, such that uncolonized locations had a higher coverage of PA than those that were colonized. However, this relationship did not remain significant after Bonferroni corrections were applied. In addition, the colonizations of five (four after Bonferroni corrections) southern species were at significantly higher altitudes than uncolonized sites. Although bittern was found to colonize significantly lower altitude sites, this did not remain significant after Bonferroni corrections. Colonizations were sometimes at lower latitudes than uncolonized sites; three species showed a significant negative relationship at $P < 0.05$, although

Table 3. Results from the mixed effects models

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 (0.000002)**	**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**

N, number of 1-km² locations included. For each explanatory variable (PA, percentage of protected area; Altitude, mean altitude of 1-km² grid square; Latitude, Y co-ordinate of centre of 1-km² grid square in km), we give the coefficient of the relationship and the standard error of the coefficient in parenthesis, along with the *P*-value associated with each. Values shown in bold are significant at $P < 0.05$.

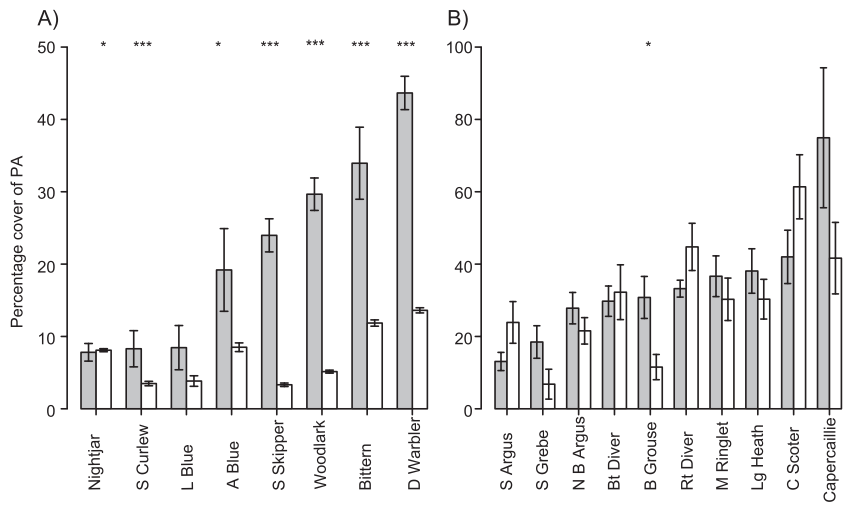

Figure 1. The mean percentage cover of protected areas (PA) in 1-km^2 grid squares for each species (A) with records of colonization (grey bars) or that were uncolonized (white bars) and (B) with records of persistence (grey bars) or where the species went extinct (white bars). Also presented are the SEM; significance: *$P < 0.05$; *** $P < 0.001$.

only the silver-spotted skipper remained significant after Bonferroni corrections. Thus, in contrast to northern species when analyses individually, PA status was important for colonization 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 colonization (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 colonizations occurred in squares at higher altitudes, and latitude, such that colonizations 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 colonization 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 is perhaps not surprising, given that populations located further south and at lower altitudes will have experienced higher levels of stress as a result of climatic change. However, when species were analyzed individually, only one (black grouse) of ten northern species showed a significant positive relationship between percentage 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 a result of the lack of power to allow inclusion of interaction terms, rather than a lack of effect. However, it is somewhat in agreement 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, although 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 (Carroll *et al.*, 2011; Pearce-Higgins, 2011), and more work is required to test the generality of this finding. Because not all SSSIs are under active management, the effectiveness of PA management could not be determined here. More detailed data on the impacts of management regimes, comparing managed areas with unmanaged locations, would help to determine whether 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 minimize 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) identified 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.

Colonized 1-km^2 locations had higher PA coverage than locations that remained uncolonized 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 colonization 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 the present study shows that this effect was not simply a result of location of PAs at higher altitudes and latitudes within Great Britain, namely the locations that would become more suitable during climatic change. The positive effect of PA designation on colonization may be the result of a lack of suitable habitat outside PAs, rather than active management or protection in PAs *per se* (Pearce-Higgins & Green, 2014), although informed management has been demonstrably important in the recovery from 1990 onward for the three southern butterfly species studied here (Thomas, Simcox & Hovestadt, 2011; Lawson *et al*., 2014a; O'Connor, Hails & Thomas, 2014). We were unable to differentiate uncolonized and colonized 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 reported in the present study.

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 colonized 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 colonized 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 the result of a 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^2 grid cells than climatic differences between them. Although the negative effect of latitude on colonization 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 colonized and uncolonized species (see Supporting information, Tables S1, 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') (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 the analyses reported in the present study are limited to birds and butterflies, these two taxa are disproportionately considered when designating PAs in Britain and elsewhere. In addition, existing PAs might be expected to be even more important for retaining species with lower dispersal abilities from other taxonomic groups.

Although individual PAs may lose some of the features for which they are currently designated as a result of climatic change (Hole *et al*., 2009; Araújo *et al*., 2011), 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; present 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 (Leach, Zalat & Gilbert, 2013). In heavily human-modified countries such as England, PAs represent the majority of suitable semi-natural locations that could be colonized (Lawton *et al*., 2010) and degazettement subsequent to a loss of feature species could result in an overall reduction in the area of semi-natural vegetation as a result of conversion to other uses. In the 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 colonization 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). Because PAs appear to both retain northern species and facilitate the spread of species, we suggest that PA management should be designed with climatic change in mind to either slow the retreat or aid the spread of species. However, the contribution of management actions within PAs to achieving these goals is still largely unknown, and so effective monitoring systems across the PA network as a whole should be introduced to fill this knowledge gap.

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. We thank two anonymous reviewers for their helpful comments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Generalized linear model results for species with records of colonization, where a response of 0 is locations that were not colonized and 1 is locations that were colonized, with randomly selected equal number of uncolonized squares. 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 parenthesis, along with the *P*-value associated with each. Values shown in bold are significant at $P < 0.05$.
Table S2. Results from the mixed effects models with equal numbers of uncolonized and colonized locations for the southern species. *N*, 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 parenthesis, along with the *P*-value associated with each. Values in shown bold are significant at $P < 0.05$.

