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The effectiveness of the protected area network of Great Britain

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ABSTRACT

Protected Areas (PAs) are core components of conservation strategies, but the networks they form are rarely assessed for their effectiveness over time. We tested different aspects of effectiveness of the British PA network in achieving long-term biodiversity outcomes, including species representativeness of initial location choices and network resilience (in terms of species persistence). Using 10 × 10 km cells, 'landscapes', with contrasting cover of protected areas managed specifically for biodiversity conservation, we evaluated these aspects of effectiveness by analysing species distribution changes of over 2800 species of animals and plants from 1974 to 2014. Landscapes that contained PAs in 1974 had higher species representativeness than landscapes without PAs, but landscapes with low PA coverage (<median) were more representative than those with high PA coverage (>median). Many species distributions have declined since 1974, and the distributional trends of declining and priority species were similar (on average) in landscapes containing PAs and in the wider countryside, implying PA-containing landscapes were not resilient to landscape-scale pressures. Nonetheless, PAs did have a small positive impact over time on landscape-scale representation trends of declining species, and priority species. Regardless of PA coverage, topographically heterogeneous landscapes were more likely to retain priority species between 1974 and 2014, and less likely to be colonised by expanding species. Despite landscapes with low PA coverage disproportionately contributing to overall PA network representativeness, they are less resilient than landscapes with high PA coverage, which jeopardises their value in the long-term and will require landscape-scale habitat conservation and restoration to address.

1. Introduction

Species declines continue globally (Pimm et al., 2014; Ceballos et al., 2015; Secretariat of the Convention on Biological Diversity, 2020), and conservation efforts to prevent them have been largely unsuccessful (Hoffmann et al., 2010; Johnson et al., 2017). Protected areas (PAs) are one of the main area-based tools to combat species loss, by preventing or limiting changes to land use and other pressures that are causing declines outside PAs (Watson et al., 2014; Maxwell et al., 2020). Global terrestrial PA coverage currently stands at 15% (Stokstad, 2020; UNEP-WCMC and NGS, 2020), and a coverage target of 17% by 2020 agreed under the Convention on Biological Diversity Aichi Target 11 (CBD, 2010) has been missed. Although PA extent is increasing, and higher coverage targets are likely as part of the post-2020 global biodiversity framework (Bhola et al., 2021; CBD, 2020), assessing the effectiveness of PA networks (the set of all PAs within an area) is essential in understanding the degree to which they contribute to the long-term conservation of nature. This requires a multi-faceted evaluation of all component PAs of the network: both of initial establishment locations, usually in terms of representativeness of species or habitats; and the extent to which long-term biodiversity outcomes are achieved through appropriate management and PA network design (Rodrigues and Cazalis, 2020).

Previous evaluations of protected area network effectiveness have primarily focused on evaluating PA extent and locations, through identifying network representativeness, rather than biodiversity outcomes which require evaluation over time (Butchart et al., 2015; Maxwell et al., 2020). For a PA network to be effective initially, component PAs must be 'representative': located in areas that support the full variety of species and/or habitat diversity, in order to be able to

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conserve the full range of species in a region or country (Margules and Pressey, 2000). Current representativeness may be used to identify missing or underrepresented 'features' (usually populations, species, ecosystems, but may include cultural and ecosystem service targets too) so as to recommend improvements (Oldfield et al., 2004; Shwartz et al., 2017; Fonseca and Venticinque, 2018). Systematic Conservation Planning (SCP) is often used to improve network representativeness by prioritising areas that maximise 'complementarity' using spatially-explicit methods, whereby proposed additions (priority areas) to a PA network disproportionately add underrepresented biodiversity features (Wilson et al., 2009). SCP enables a rigorous and accountable way of allocating funds to protect a coherent network of PAs, through planning to optimise the ability to meet overarching conservation goals (Margules and Pressey, 2000; Kukkala and Moilanen, 2013), and may include informative planning layers in addition to biodiversity data (Magris et al., 2018). Evaluating representativeness (representation of the full variety of biodiversity within the PA network (Kukkala and Moilanen, 2013)) is important, but it is only one facet of long-term nature conservation, and understanding biodiversity outcomes through time is ultimately just as important in evaluating network effectiveness (Nicholson et al., 2006; Rodrigues and Cazalis, 2020).

As well as representing biodiversity, a PA network should retain initial conservation value through reducing habitat loss and maintaining species populations (Watson et al., 2014) but evidence for the ability of individual PAs to deliver these long-term biodiversity outcomes is limited (Rodrigues and Cazalis, 2020). There is support for PAs conserving habitat, especially forest cover (Geldmann et al., 2013; Spracklen et al., 2015), even though pressure on PAs has actually increased since the turn of the century (Geldmann et al., 2019). However evidence for maintaining species populations is more mixed: better outcomes for species richness and abundance have been reported (Coetzee et al., 2014; Cazalis et al., 2020), but other studies have found this benefit largely explained by land use and habitat type (Gray et al., 2016; Pellissier et al., 2020), or no benefit at all (Rada et al., 2019). Additionally, when evaluating an entire PA network it is important to evaluate overall biodiversity outcomes across the network, rather than individual site-specific ones: many PAs are established to protect a single species or community and may keep to these limited targets well, but the network as a whole may fail to be effective if biodiversity outcomes are poor overall across the covered area. A number of factors have been proposed to improve long-term PA network outcomes, including increasing area of protection (Isaac et al., 2018), improving connectivity (Saura et al., 2014), incorporating topographic heterogeneity (Oliver et al., 2010), and strengthening law enforcement (Hilborn et al., 2006). Furthermore, although SCP approaches facilitate improving initial representativeness, evidence that they also increase effectiveness in maintaining long term outcomes, through location and design factors improving the resilience of PA networks, is lacking (McIntosh et al., 2018; McIntosh, 2019).

Quantifying long-term biodiversity outcomes across entire PA networks over time is inherently difficult. Evaluations can simulate future outcomes based, for example, upon species persistence (Nicholson et al., 2006), projected distributions (Stralberg et al., 2015) or modelled future abundance (Johnston et al., 2013). Although these evaluations raise important considerations in PA network planning, they do not consider how effective a PA network has been in achieving outcomes to date across a broad range of taxa (Bottrill and Pressey, 2012) and they are a product, ultimately, of the predictive models used and not empirical observation. The gold standard of long term monitoring of PA outcomes is conservation 'impact' evaluation, which involves comparing outcomes in 'identical' paired sites through time, one with a conservation intervention and one without, to measure the positive effect of the PA (Pressey et al., 2015, McIntosh et al., 2017). Although this is possible for individual or small numbers of PAs, it is not practical when considering an entire PA network, and other retrospective methods are needed to evaluate outcomes (Sacre et al., 2020). Long-term outcome evaluation is still possible for PA networks through analysing variation in long-term species distribution datasets. A network's resilience in maintaining representation of populations over time, through increased meta-population persistence against wider landscape threats, can be assessed and hence another measurable aspect of network effectiveness (Gaston et al., 2006; Isaac et al., 2018). As well as overall PA network resilience, robust analysis of representation over time would also permit an evaluation of the impact of PAs on achieving these long-term biodiversity outcomes, and support policy-makers to make evidence-based conservation decisions (McIntosh et al., 2017).

The PA network of Great Britain (GB) is extensive, with >10,000 current statutory terrestrial PAs and many different protection categories (Gaston et al., 2006). National Nature Reserves (NNR) and Sites of Special Scientific Interest (SSSI) formed the initial designation structure of the network, as they focus on species and habitats (and in some cases geological or geomorphological features). Sites with more recent designations, such as those under the Natura 2000 network, are usually also SSSIs. NNRs and SSSIs were historically largely selected based upon habitat representation (Ratcliffe, 1986). The process of selecting NNR and SSSI sites involved finding high quality areas of habitat that were typical of climatic, physiographic, edaphic and anthropogenic variation within those habitats. The quality of the site itself was based on a range of criteria including size, diversity, naturalness, typicalness, and fragility, and sites were then graded and assigned NNR or SSSI designations depending upon importance (see Ratcliffe (1977) for full description). Although site selection was methodical and aimed at being representative, species-level complementarity was not considered explicitly: as such it cannot be considered a systematically planned network, as understood today.

The government's 25 Year Environment Plan (25YEP) (DEFRA, 2018) creates a context of policy change for England that presents an important opportunity to evaluate the current network performance, and to use this to inform and improve the selection of new sites for conservation action. The 25YEP envisages moving to a landscape scale approach, with a Nature Recovery Network (NRN) at its core, but also the commitment to create 500,000 ha of new priority habitat and plant millions of trees in England (DEFRA, 2018). Similar commitments are to be found in current and proposed legislation and biodiversity strategies in Wales and Scotland (Duigan et al., 2020). Investigating the effectiveness to date of the existing GB PA network, as well as evaluating improvements that could potentially be achieved by using SCP, would contribute useful insights to the forthcoming implementation of the 25YEP and similar conservation strategies.

Here, we evaluate how the changing distributions of species relate to the distributions of PAs managed for biodiversity conservation (SSSIs and NNRs) at a 10 × 10 km spatial resolution (which we refer to as 'landscapes') as designated in 1974, to reflect an historic baseline shortly after the bulk of the GB PA network had been created. We assess network effectiveness through both the initial representativeness, representation of species across the PA network at that time; and its resilience, by analysing subsequent changes to the distributions of species in PA-containing landscapes though to 2014. We further evaluate whether a PA network based on SCP would have initially performed better, in terms of higher species representativeness than the actual network. We predicted that PA locations would initially be well sited (i.e. have greater species representation than landscapes that lacked PAs), and that there would be higher levels of species representation in landscapes with greater PA coverage, but also that species representation could have been initially significantly improved through the use of SCP. We also expected that landscapes containing PAs, and particularly landscapes containing larger areas of PA land, would be most resilient in maintaining species distributions over time, compared to landscapes without PAs. Additionally, in order to investigate potential drivers of landscape resilience in GB in greater detail, we divided the UK into 100 × 100 km regions and tested the importance of different factors associated with resilience within them. These included level of protection in each landscape, to evaluate PA impact over time, and also overall regional connectivity and topographic roughness. Finally, we included regional similarity of the actual PA network to an optimised SCP network as a factor, to test if regional PA configurations matching SCP priorities were more resilient.

2. Methods

In order to investigate different facets of PA network effectiveness within Britain, we firstly calculate the initial representation of species within protected and non-protected landscapes at a baseline date (representativeness), and then how this representation has changed over time up to the present (resilience), based on recorded species distribution changes. An optimised national network was also created using systematic conservation planning software to investigate how its species representativeness compares to the actual network. Finally, to investigate potential drivers of resilience, we model current landscape representation on a regional scale using a number of different predictors, e.g. landscape PA coverage, as well as regional connectivity, topographic roughness and similarity to the counterfactual SCP optimised network. All analysis was carried out at 10 × 10 km (henceforth ‘landscape’) resolution. An overview of the methodological workflow for assessing effectiveness is given in Fig. 1, and a glossary of terms in Table A1.

2.1. Protected areas

We defined our study area as Great Britain and associated islands greater than 20 km^2 in area. We considered the protected area network to consist of NNRs and biological SSSIs (5838 sites), as these constituted all PAs designated for the protection of biodiversity within Britain at our selected baseline date. SSSIs designated solely for geological reasons were excluded as they were not selected with biodiversity in mind, or likely to have been subsequently managed for nature conservation (912 sites). Data on the geographical boundaries and first date of notification for SSSIs were provided by Scottish National Heritage (SNH), Natural Resources Wales (NRW), and Natural England (NE) (Hinton, George; Personal Correspondence). Our study started with the PA network present in 1974, by which a large proportion of today's PA network area was already designated (Fig. A1; England: 61.1%, Scotland: 40.1%, Wales: 65.4%, total: 51.5% by area).

PAs in Britain are typically less than 10 km^2 in area (Fig. A2) and when aggregated into 10 × 10 km cells (landscapes), PA landscape coverage is heavily skewed to lower levels of protection (Fig. A3). Hence, landscapes were split into the following 3 protection categories and assessed separately in both the national and regional analyses; ‘PA absent’ where there were no protected areas in a given landscape, ‘low PA coverage’ cells had less than the median PA coverage by area (up to 1.39% landscape protected), and ‘high PA coverage’ cells had more than median coverage (1.39–90.91% landscape area protected).

We undertook a sensitivity analysis by repeating our analyses using 40% and 60% PA coverage quantiles (0.89% and 2.39% absolute landscape coverage respectively) as a cut-off instead of the median (1.39% coverage). Additionally, as these were all objectively low levels of protection, we also repeated the analysis for the higher 80% quantile

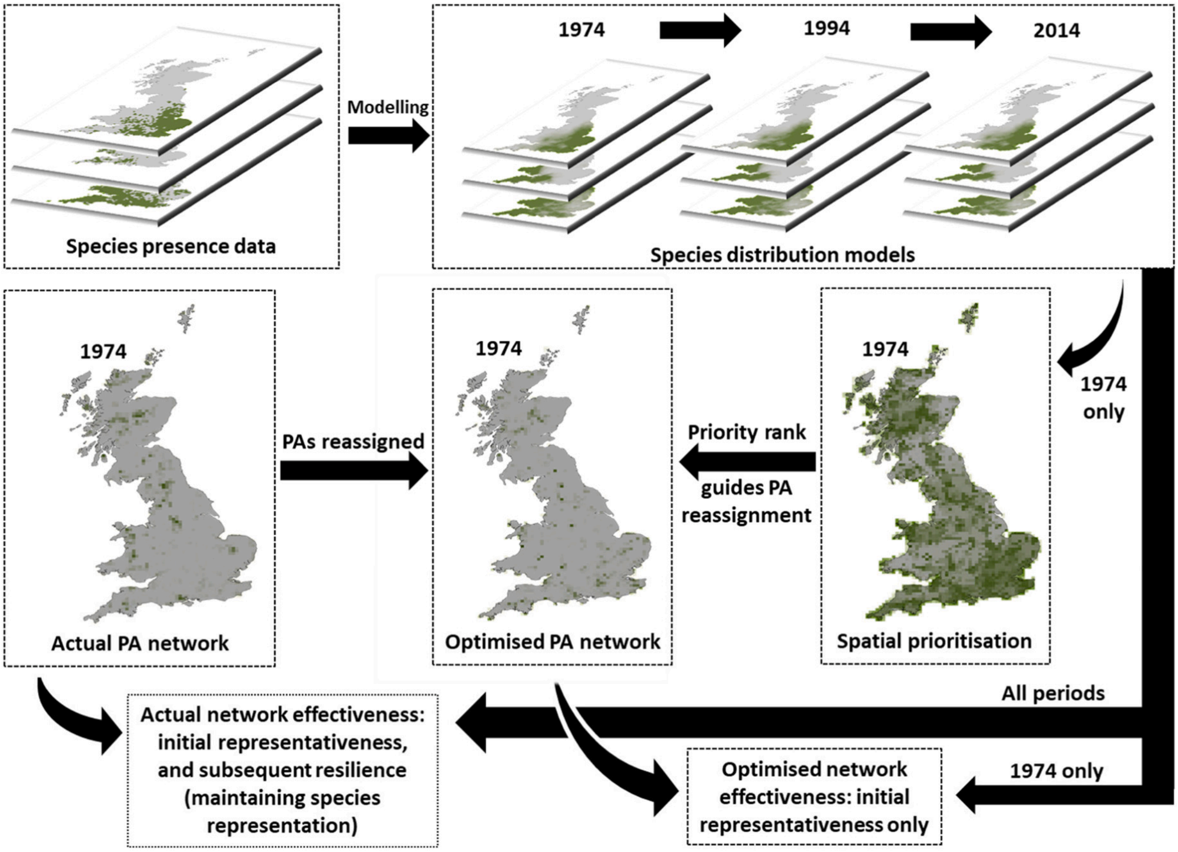


Fig. 1. Study methodology workflow for national PA network effectiveness analysis. We spatially modelled species presence data, based on bioclimatic variables, and mapped the PA network as it existed in 1974. Only sites managed specifically for biodiversity conservation (SSSIs and NNRs) were included in the PA network. Effectiveness was assessed firstly from initial national representativeness, calculated in 1974 from summed species distributions within different PA categories. We then compared this to species representation in subsequent periods in 1994 and 2014 to investigate long-term PA network resilience. An optimised network was created that would have been selected in 1974, using up-to-1974 species distribution data, had SCP conservation prioritisation software been used to determine selection. We then used this optimised counterfactual to compare initial representativeness with the actual PA network. Additionally, not shown in figure, mean landscape representation in 100 × 100 km ‘regions’ was modelled to investigate predictors of landscape resilience.

(8.20% coverage). Results were consistent with those in the main text (Tables A4–12) and only reported in the main text if they differ.

2.2. Species distributions

Historic distribution data were provided by a number of recording organisations including Biological Records Centre (BRC) and Butterfly Conservation (BC), and breeding bird distributions (Gillings et al., 2019) from British Trust for Ornithology (BTO). We were able to include a total of 4855 species distributions in the analysis as they were present in all three periods, from a total of 11 taxonomic groups (Table A2). Species not present for every time period were not included (174, 404, and 572 species for periods 1, 2, and 3 respectively) to remove inconsistently monitored species, but this also resulted in species GB extinction and colonisation events being excluded. Species distributions were in the form of annual presence records.

Our study started in 1974 when recording activity in a number of taxonomic groups was well established (Period 1). We identified monitoring points at 20 year intervals in 1994 (Period 2) and 2014 (Period 3) when we measured changes in species representation over time. Due to differences in recorder effort between time periods we calculated sampling periods (Table A3) for each taxonomic group, except birds and vascular plants (atlas data were only available for specific time periods in birds (1968–72, 1988–91, 2007–11), and vascular plants (1930–69, 1987–99, 2010)). We took all records during the monitoring point year and then successively added data from previous years for each species separately, stopping when the number of new landscapes added to the cumulative species distribution was below 5%. The median species sampling period was used as the taxonomic group's sampling period.

For each species with over 10 presence records (3452 species) we interpolated their range using Integrated Nested Laplace Approximations (INLA) in the inlabru package (Bachl et al., 2019) for each period. A joint model of distribution intensity and recording effort was used, including four biologically relevant covariates: seasonality, growing degree days, water availability and winter cold (see Beale et al. (2014) for details). Soil pH was additionally included as a covariate for butterfly, moth, and vascular plant models as it can have a strong influence on plant distribution (Barbour et al., 1987), and hence dependent lepidopteran species. We calculated the biologically relevant covariates using climate variables obtained from the Met Office (Centre for Environmental Data Analysis, 2017), specifically mean temperature, sunshine and rainfall. We then extracted monthly means of the weather data for 10 year intervals preceding each period date. Soil pH used in the models was obtained from Countryside Survey datasets; dated 1978, 1998, and 2007 for each period respectively (UK Soil Observatory, 2007). We also used soil moisture in the calculation of water availability (Batjes, 1996).

To estimate recorder effort we needed broad habitat layers which we extracted from the Countryside Survey datasets: for 1974 (Period 1), we used the 1978 Countryside Survey dataset (Sheail and Bunce, 2003); for 1994 (Period 2), Land Cover Map 1990 (CEH, 1990); and for 2014 (Period 3), Land Cover Map 2015 (CEH, 2015). The habitat layers were then used in a Frescalo analysis (Hill, 2012) to estimate recorder effort by comparing species records within each landscape to its neighbours, weighting for spatial proximity and habitat similarity. Recording effort was calculated for each taxonomic group for each period separately. 2687 species models converged. Although undertaking model cross-validation was not possible due to the large number of models, models predictions were tested using the area under curve (AUC) of the receiver operating characteristic (ROC) approach (Araújo et al., 2005; Bahn and McGill, 2013) and found to be a fair approximation of actual species distributions for the given time period within Britain (AUC: period 1 mean = 0.836, SD = 0.124; period 2 mean = 0.834, SD = 0.120; period 3 mean = 0.829, SD = 0.122). In order to include species with genuinely restricted distributions, rather than species with very low recorder effort, we included un-modelled presence records for the species without converged models when there was greater than 50% spatial overlap between chronological periods. This resulted in a final total of 2861 species being included in the effectiveness analysis (Table A2).

2.3. Evaluating effectiveness

Factors contributing to overall PA network effectiveness were assessed differently. The initial effectiveness in the establishment of PA locations was assessed through representativeness soon after original designation (period 1). We used this initial species representation as a baseline for evaluating resilience (i.e., ability to maintain representation over time). Representation of each species in each time period was calculated as the summed modelled presence within each of the three PA categories (landscapes with zero, <median PA, or >median PA cover). As the number of landscapes differed between PA categories we normalised this to compute representation per landscape. We computed this measure of representation for each PA category in all 3 periods, and repeated the analysis for: (1) ‘all species’ (2861 species); (2) ‘declining species’, species with ranges that contracted over the study period (1362 species); (3) ‘expanding species’, species with ranges that expanded over the study period (1463 species); and (4) ‘priority species’, any species listed under Section 41 (S41) of the 2006 Natural Environment and Rural Communities (NERC) Act (179 species).

In order to test potential benefits of SCP, we carried out spatial prioritisation for GB landscapes as though it had been conducted in 1974 (with the 2861 ‘all species’ distributions from 1974) using Zonation (Moilanen, 2007). This spatial prioritisation produced a complementarity-based ranking of conservation priority over GB which we used to create a counterfactual ‘optimised’ PA network (i.e., as if the same total PA area had been allocated using Zonation in 1974). We created this by reassigning PAs using the 1974 baseline spatial prioritisation rank (‘optimised’ sites) such that the largest protected area coverage was assigned to the highest priority hectad, the second largest to second highest priority etc. Hence both real and optimised PA networks had exactly the same distribution of landscape PA coverage (Fig. A4). Species representativeness could then be assessed for the initial period in the optimised and the actual PA network.

We carried out analyses at two spatial scales. The analyses described so far considered different aspects of effectiveness using all 10 × 10 km cells across GB. However in order to further investigate drivers of landscape resilience, and because species distribution trends and PA designation vary geographically, we carried out a second set of analyses in which 10 × 10 km cells were nested within ‘regions’. Each region consisted of a 100 × 100 km sample, incrementing in 50 km latitudinal and longitudinal steps, with spatial non-independence accounted for in later modelling. Only regions with greater than 50% land coverage that had at least one landscape from each PA category were considered (106 overlapping regions). In each region representation was aggregated into a single metric for each PA category separately, and this was calculated as the mean species representation per landscape within the PA category (henceforth ‘mean representation’). This analysis also allowed us to investigate the impact of protection by comparing resilience trends within protected and unprotected 10 × 10 km cells within and between regions. The analysis was repeated for the same categories of species (all, declining, expanding, and priority) used for the national analysis.

To identify factors driving landscape resilience, a Bayesian conditional autoregressive spatial regression analysis was undertaken using *INLA* (Lindgren and Rue, 2015). We fitted a model with regional mean representation in the most recent period (Period 3 – 2014) as the dependent variable (*r*). We also included representation during the baseline period (Period 1 - 1974) (*base_rep*) as a predictor variable to control for initial representation, thus allowing *r* to function as a proxy for resilience. Other predictor variables included protection category (zero, <median PA, >median PA) as a categorical variable (*PA_cat*) to investigate PA impact, and the change in regional PA coverage from the baseline (1974) to current (2014) period (*PA_change*) to control for later additional protection (Fig. A1). Other regional covariates expected to influence resilience were also included with interaction terms with the protection category; PA connectivity, topographic heterogeneity, and similarity between actual network configuration and SCP optimised network (Eq. (1)). We computed the PA connectivity (*PA_conn*) within a region as the inverse of the median nearest neighbour edge to edge distances between PAs (Calabrese and Fagan, 2004), and we calculated similarity to optimised network (*PA_sim*) as the Spearman's rank correlation between actual and optimised PA distribution. We computed topographic roughness (*Topo*) as the standard deviation of elevation (SD across 30 m cells within each region). We obtained elevation data from Google Earth Engine, using the ALOS DSM: Global 30 m dataset (Takaku et al., 2016).

$$logit(r_i) = b_o + b_1 \times PA\_cat_i \times (b_2 \times PA\_conn_i + b_3 \times PA\_sim_i + b_4 \times Topo_i) + b_5 \times base\_rep_i + b_6 \times PA\_change_i + SE_i \tag{1}$$

where $logit(r_i)$ is the mean representation in region i within a given PA category, PA_cat_i, included as a categorical variable. PA_conn_i is the connectivity between PAs in the region, PA_sim_i is the correlation between actual and optimised PA distribution within the region, $Topo_i$ is the regional topographic roughness, $base\_rep_i$ is the initial representation at period 1 for the PA category (PA_cat_i) and PA_change_i is the change in protection coverage area from baseline to current period within the region. SE_i is the structured and random spatial effect for region i, b_0 is the intercept, and $b_{1\text{-}6}$ are the estimated parameters for the corresponding covariates.

3. Results

3.1. National PA network effectiveness

These analyses consider initial PA network effectiveness in achieving long-term conservation outcomes though the network's starting representativeness, and subsequent resilience through the extent species representation was maintained. This was undertaken across the whole of GB, split into three landscape categories (10 × 10 km cells containing zero, <median PA and >median PA coverage by area), and repeated for four categories of species (all, declining, expanding, and conservation priorities).

Baseline PA locations were ‘well chosen’, as landscapes with protection typically had higher representation of priority species per landscape than ‘PA absent’ areas (Wilcoxon signed-ranks, two-tailed: Absent-Low: median = 0.327–0.477, $Z = -9.000$, $P < 0.001$; Absent-High: median = 0.327–0.385, $Z = -8.942$, $P < 0.001$; Fig. 2). Unless otherwise stated results reported are from the ‘priority species’ category since these are the main targets for conservation, and hence most closely reflect conservation priorities. We found comparable results for every species category (Table A4), with the exception that the landscapes with highest PA coverage (80% quantile ‘high PA’ areas) did not have higher priority species representation than ‘PA absent’ landscapes (Table A10).

If SCP had been used at the baseline date, optimised through spatial prioritisation using Zonation, the initial network representativeness would have improved. Initial representation per landscape would have been increased slightly for ‘high PA’ category protected areas (Wilcoxon signed-ranks, two-tailed: High PA Actual-optimised: median = 0.385–0.451, $Z = -7.764$, $P < 0.001$ two-tailed; Fig. 3). Due to the ‘high PA’ landscapes being assigned to optimal areas more efficiently, the optimised ‘low PA’ category in fact had lower representation (Wilcoxon signed-ranks, two-tailed: Low PA Actual-Optimised: median = 0.477–0.404, $Z = 8.383$, $P < 0.001$; Fig. 3). These patterns were seen for all categories of species (Table A5).

Surprisingly, ‘low PA’ landscapes had higher initial representation of species distributions than ‘high PA’ landscapes, and this pattern

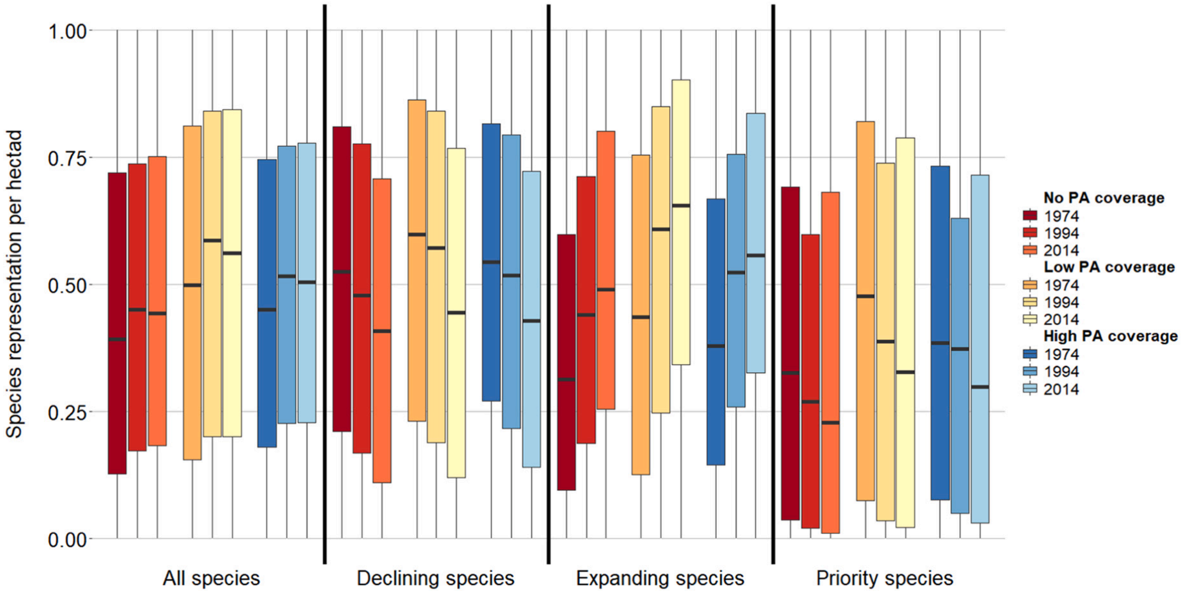


Fig. 2. Representation per landscape within different GB PA categories of 4 different categories of species: all species ($n = 2861$), declining species ($n = 1362$), expanding species ($n = 1463$), and priority species ($n = 179$). Species were assessed within each PA category (colours - ‘PA absent’, ‘low PA’ and ‘high PA’) for each of the three periods (dark to light shading through time – 1974, 1994, 2014) to investigate initial representativeness, and resilience through changes in representation over time. The lower and upper borders of the box are lower and upper quartiles, respectively; the horizontal bar is the median; and whiskers represent the lowest and highest observations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

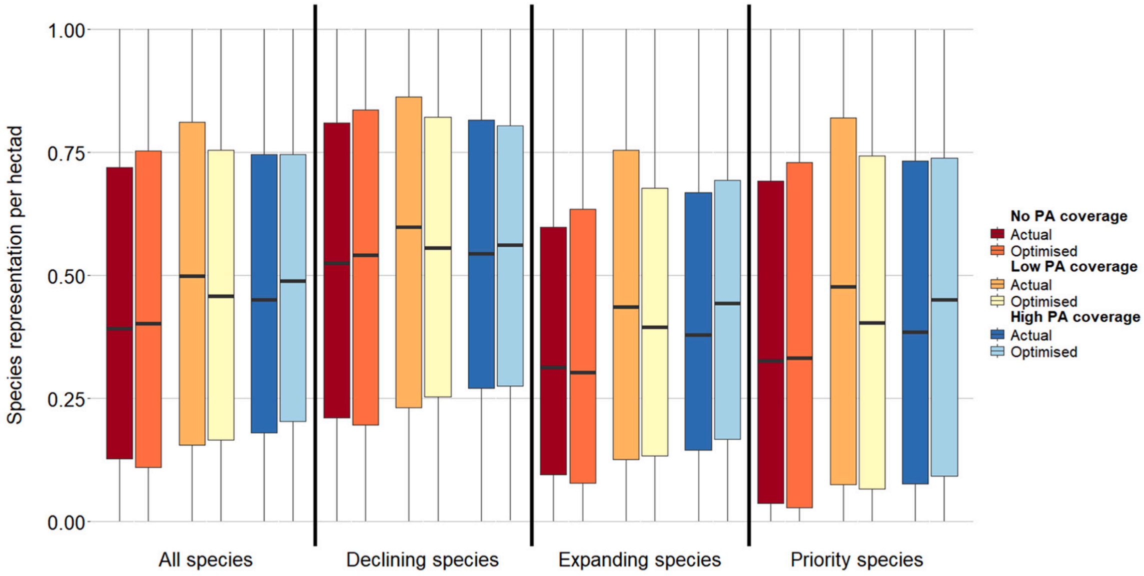


Fig. 3. Initial representation per landscape of the actual PA network, and the optimised PA network, for period 1 (1974). Species were assessed within each protection category categories (colours - 'PA absent', 'low PA' and 'high PA') for both the actual (dark shading) and optimised network (light shading). The lower and upper borders of the box are lower and upper quartiles, respectively; the horizontal bar is the median; and whiskers represent the lowest and highest observations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

continued through time (Wilcoxon signed-ranks, two-tailed: 1974 Low-High: median = 0.477–0.385, $Z = 5.972$, $P < 0.001$; 1994 Low-High: median = 0.388–0.373, $Z = 5.367$, $P < 0.001$; 2014 Low-High: median = 0.328–0.298, $Z = 3.497$, $P = 0.001$; Fig. 2). In fact every PA category showed similar temporal trends in representation (Fig. 2). This meant initial differences between PA categories remained for subsequent periods (Table A4) and, thus, PA-containing landscapes did not appear to be more resilient than unprotected ones at maintaining populations of declining and priority species at the national scale.

Priority species declined consistently over time, whereas 'all species' increased between the first two periods (Fig. 2). This resulted in an overall net gain in representation per landscape of 'all species' for each PA category (including for zero PA landscapes) from the 1974 baseline to the present 2014 period (Wilcoxon signed-ranks, two-tailed: PA absent 1974–2014: median = 0.393–0.444, $Z = -7.336$, $P < 0.001$; Low PA coverage 1974–2014: median = 0.498–0.561, $Z = -4.854$, $P < 0.001$; High PA coverage 1974–2014: median = 0.451–0.504, $Z = -7.006$, $P < 0.001$; Fig. 2).

Representation trends varied between species within PA landscape categories in Britain, which when considered together produce the previously reported results. In some species, distribution contraction was less severe in landscapes in the 'high PA' category; for example European nightjar *Caprimulgus europaeus* distribution contracted 53.3% in PA absent landscapes, but only 37.9% in 'high PA' landscapes. However, representation of some species in fact declined more in landscapes with protected areas, such as brown hairstreak *Thecla betulae* which contracted 70.5% in PA absent landscapes, but 74.2% in 'high PA' landscapes. In this case, other factors with a regional basis are driving change which protection cannot offset. Further illustrative species and distribution maps are provided in Fig. A5.

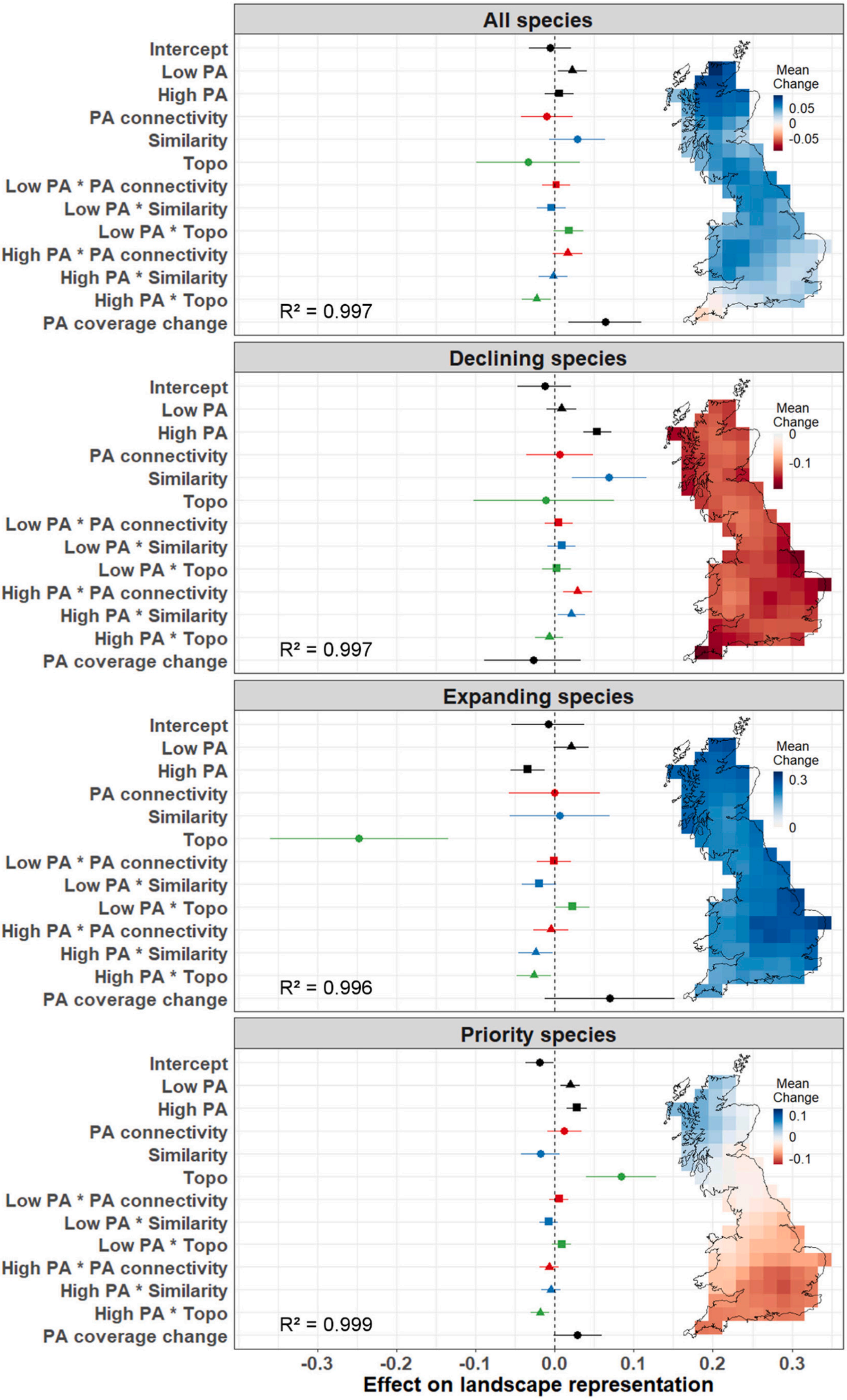
3.2. *Predictors of landscape resilience*

The regional analyses again considered long-term effectiveness for GB 10 × 10 km 'landscapes', but we now investigated the drivers of resilience through modelling representation outcomes within 100 × 100 km 'regions'. Landscapes-within-region are still split into the same three protection categories and we repeated the analysis for all, declining, expanding and priority species. Baseline representation had a large positive effect on current representation for every species category (All species: effect size = 0.863, Credible Interval (CI) = 0.821, 0.906; Declining: effect size = 0.746, CI = 0.677, 0.819; Expanding: effect size = 0.752, CI = 0.712, 0.792; Priority: effect size = 1.088, CI = 1.051, 1.125; Table A12). Hence the results for the other variables indicate their effects on change in representation through time, i.e. impact on resilience, controlling for baseline variations in diversity and spatial effects.

For our analysis of factors driving resilience, in terms of PA impact we found strong support for correlations between 'high PA' landscapes and more positive trends of declining (effect size = 0.054, CI = 0.036, 0.072) and priority species (effect size = 0.028, CI = 0.016, 0.041), but a negative effect on expanding species (effect size = −0.034, CI = −0.055, −0.012, Fig. 4). 'Low PA' landscapes also had positive, but weaker, association with priority species trends (Fig. 4; effect size = 0.020, CI = 0.008, 0.032).

Regions that matched the optimised SCP network configuration more closely also had improved declining species trends (effect size = 0.069, CI = 0.022, 0.117, Fig. 4). PA connectivity had a small positive effect on 'high PA' landscape declining species trends (effect size = 0.029, CI = 0.011, 0.047). Additionally, topographic roughness was strongly positively associated with priority species trends, and negatively with expanding species (Fig. 4; effect size = 0.084, CI = 0.040, 0.128, and; effect size = −0.247, CI = −0.360, −0.135, respectively).

Despite the overall difference in landscape resilience between PA categories, spatial trends in representation change between regions were largely similar between PA categories (Fig. A6). Only the 'PA absent' category (Fig. 4, inset map) is described here, as it is the intercept of the regression models. There were slight declines in south-west England for 'all species' representation but increases in the rest of Britain (Fig. 4, inset map). The trends for declining and expanding species were opposite, with western Scotland and East Anglia having a particularly large decrease in declining species and large increase in expanding species representation. There was clear north-south spatial structuring for priority species representation change, with northwest Scotland increasing whereas representation decreased in the majority of England.



(caption on next page)

Fig. 4. Factors affecting landscape (10 × 10 km) resilience at maintaining species representation in 100 × 100 km square regions across GB. We carried out spatial regression analysis on 4 different species categories (all, declining, increasing, and conservation priorities), with mean PA category representation per landscape (10 × 10 km square) in period 3 (2014) within the region included as the dependent variable. Baseline representation in period 1 (1974) was controlled for by including it as a covariate in the model (not plotted), and this allowed the dependent variable to function as a proxy for landscape resilience. 'Low PA' and 'high PA' are factorial covariates in the models (triangle and square points respectively). All other covariates are continuous (colours: connectivity – red, similarity to optimised network – blue, topography – green, and change in PA coverage between periods 1 and 3 - black). Points indicate the mean effect size, and horizontal lines the credible interval. Spatial trends between regions are also shown (inset maps) with change in mean representation for individual regions (period 3 – period 1) plotted for each species category. Only the 'PA absent' protection category spatial trends are presented as it is the intercept factor for the model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

We found that PAs managed for biodiversity conservation were initially well sited, in the sense that landscapes containing PAs had higher species representation than 'PA absent' landscapes in 1974, and these 'protected landscapes' still had relatively good species representation in 2014. However, we found that species declined (or increased) in generally similar ways, averaged across landscapes that either did or did not contain PAs. Nonetheless, when we controlled for regional differences (i.e. considering landscapes within and between regions), our analyses revealed weak tendency for 'high' (and to a lesser extent 'low') PA coverage to have a positive impact on landscape representation outcomes for declining and priority species through time – a conservation benefit.

4.1. *Effectiveness: baseline representativeness*

Our results agreed with previous studies that the initial PA locations in Britain were picked well overall (Rodrigues et al., 1999; Hopkinson et al., 2000), somewhat validating the original site selection strategy (Ratcliffe, 1977) which, although not as efficient or representative as a SCP approach, had significantly higher species representation in 'protected' landscapes than in unprotected ones. However, landscapes with the very highest PA coverage (in the upper 80% quantile) did not have higher priority species representation than unprotected landscapes, primarily because 'high PA' landscapes are mainly located in relatively low diversity regions in north-western and upland Britain (Shwartz et al., 2017).

Landscapes with low protection had the highest initial species representation, highlighting the relatively important contribution of small PAs to conservation networks (Wintle et al., 2019). This likely reflects national patterns of species distributions and habitat fragmentation. Species with restricted distributions, and species richness as a whole, tend to be concentrated in southern and lowland Britain, reflecting climatic and soil factors, but there is a smaller amount of semi-natural habitat there, as a consequence of a greater intensity of agriculture amongst other factors (Oldfield et al., 2004). Hence lowland priority species often occupy small sites in fragmented 'low PA' landscapes (Figs. A1, A4).

If a SCP strategy had been used nationally in 1974 to designate PAs, with the distribution data available at the time, then this spatially optimised historic counterfactual network would have significantly higher initial representativeness than the actual PA network. For example, priority species median representation in 'high PA' landscapes would have increased by 6.6%. The largest differences between the actual and optimised network were decreases in 'low PA' and corresponding increases in 'high PA' representation; echoing that although PAs in the actual network are well distributed for species representation, 'low PA' landscapes contribute disproportionately to network representativeness. The prioritisation for this analysis was based on 'all species' distributions, however, there are many possible prioritisation considerations which can also be included, i.e. cost-efficiency, connectivity, species vulnerability, and climate change; and this would have changed the priority rank of different areas (Kullberg et al., 2015; Troupin and Carmel, 2018). The relevance and importance including these considerations could be assessed as part of a full SCP implementation.

4.2. *Effectiveness: resilience*

Despite their higher initial species representation, landscapes with protection experienced similar temporal trends in representation decline to landscapes with less or no PA coverage. These landscape trends result from a combination of factors (Hayhow et al., 2019), such as agricultural intensification (Robinson and Sutherland, 2002), climate change (Walther, 2010), or development (Hansen et al., 2005; Veach et al., 2017). These trends suggest PA outcomes have been largely due to where they were originally sited rather than because they have ameliorated declines, i.e. they are well placed but not resilient.

Whilst highlighting trends for declining and priority species, as this was the primary focus in assessing PA performance, we also note that the 'all species' analyses indicate that overall species representation for every PA category, hence species distributions, actually increased since 1974 despite a partial reversal since 1994. Other studies have found similar net positive biodiversity change globally (Dornelas et al., 2014; Daskalova et al., 2020), elsewhere in Northern Europe (Nielsen et al., 2019), and in Britain (Macgregor et al., 2019; Outhwaite et al., 2020). Spatially, these increases occurred largely in Scotland, Wales and northern England, and the spatial pattern was similar for priority species (Fig. 4 inset map). This may be driven by recent climate change allowing southern species to expand at their northern margins (Gillings et al., 2015; Mason et al., 2015). This same expansion was not seen in southern England, possibly due to the physical barrier of the English Channel, or that species colonising GB post-1974 could not be included in the analysis. Equally, species losses were generally offset by turnover in assemblage composition; regions with large distribution declines in some species often saw the largest increases in other species. This corresponded with previously identified areas of high species turnover in birds (Harrison et al., 2016).

4.3. *PA impact*

The national analysis looked at aspects of PA network effectiveness through a combination of initial representativeness, and subsequent resilience though representation trends within landscapes with different levels of protection. Although the resilience observed in Britain was poor, PAs could still have had a positive impact such that species declines would have been even more severe in those landscapes without their designation. A comprehensive impact evaluation is not possible retrospectively, and impractical for a national network, but we were able to provide a level of evaluation through the regional modelling analysis, controlling for baseline and spatial trends.

Despite following general landscape trends, PA coverage was found to have had a small positive impact on landscape resilience within regions for declining and priority species. PA coverage was associated with less negative representation trends, albeit not enough to prevent overall declines within protected landscape categories, caused by a combination of agricultural intensification, urbanisation, pollution, climate change and other factors (Hayhow et al., 2019). PA coverage within landscapes within Britain is mostly below 20% coverage (Fig. A3), and much larger protected area coverage may convey greater impact in improving resilience to these factors, or other additional benefits, but such places do not occur in Britain in numbers where these effects would be detectable in this analysis.

This analysis did not find a link between expanding species and PAs that has previously been identified in some taxa (Thomas et al., 2012; Gillingham et al., 2015), in fact 'high PA' areas had a small negative association. Although PAs can act as 'landing pads' for range-shifting species (Hiley et al., 2013), this benefit may have been missed because species colonising the GB post-1974 were not included within the analysis.

PAs in 'low PA' landscapes were found to have less positive impact than in landscapes with 'high PA' coverage at retaining representation of priority and declining species at the regional scale. This highlights the current vulnerability of landscapes with 'low PA' coverage comprising of small sites in fragmented habitat, despite their disproportionate contribution to network species representativeness. Smaller sites may have poor resilience due to higher relative management costs limiting conservation actions (Armsworth et al., 2011), smaller populations with reduced connectivity to nearby sites (Isaac et al., 2018) or a range of other factors leading to extinction debt, such that these smaller isolated populations will tend to decline over time (Watts et al., 2020). This is important when considering the expected changes in climate to which populations will have to adapt (Oliver et al., 2015; Gaüzère et al., 2016), and is urgent to address in policy if current network representativeness is to be maintained.

There are a number of approaches which could address this differential PA impact. The PA network could be optimised such that larger PAs are created in landscapes that currently have 'low PA' coverage by expanding or joining up small fragments of semi-natural habitat. Implementing this may be difficult however because of the intensity and socio-economic value of surrounding land use for other purposes, such as agriculture, and habitat creation or restoration may be required to obtain the same long-term benefit seen from 'high PA' coverage in this analysis. Thus more investment could be directed to small PA management to be put towards landscape-scale approaches, such as the establishment of non-statutory large-scale conservation initiatives (LSCIs) to buffer and link up small PAs (Shwartz et al., 2017). England is currently in the process of establishing a Nature Recovery Network (NRN), which is a key part of the 25-year Environment Plan (DEFRA, 2018), included in the forthcoming Environment Bill, and this provides an unprecedented opportunity to implement landscape-scale LSCI approaches nationally.

4.4. Other factors predicting landscape resilience

Aside from baseline representation the landscape factor most strongly predicting landscape resilience was regional topographic roughness (standard deviation of elevation), positively for 'priority species' but negatively for 'expanding species'. The increased resilience for 'priority species' can be explained by microclimatic refugia present in these areas created by microclimate heterogeneity (Oliver et al., 2010; Suggitt et al., 2018), allowing species to persist in the face of changing climatic conditions. This suggests topography should be considered in future prioritisation exercises to identify possible new sites for protection: topographically heterogeneous areas are more intrinsically resilient and so would make good candidate sites for resilient PAs, but these landscapes may not contribute as much to the representativeness of the PA network as more vulnerable flatter areas. The negative effect on 'expanding species' is more difficult to interpret, and several different processes may contribute to the observed pattern: topographically heterogeneous areas may possess more stable communities or more specialised niches, and might therefore be more resistant to new colonists; topographically diverse landscapes are, on average, at higher elevations, and hence only a small proportion of these landscapes may be suitable for expanding, heat-adapted species; and cold-adapted upland species may be unable to disperse between geographically-separated blocks of 'upland' habitats.

PA connectivity did have a small positive effect on declining species trends in 'high PA' landscapes and, interestingly, the outcomes for declining species were improved the most in regions where there was the closest match between the actual and optimised SCP distribution of PAs. Resilience of landscapes may have been improved through increased initial capacity of PAs to collectively conserve species in the long-term within these regions. Unfortunately levels of similarity within landscapes were low (range $R_s = -0.163, 0.606$) and so regions where SCP optimisation is followed more closely could not be investigated.

5. Conclusions

GB PA network representation of declining and priority species has declined over time, despite the network being reasonably well designed in terms of initial spatial configuration, albeit not in terms of PA sizes. Protected areas retain their relative importance within the landscape but undergo the same landscape effects as non-protected areas, meaning there have been similar landscape changes in species representation regardless of protection level. Although PAs have had some positive impact on priority and declining species, the network cannot be considered fully effective due to failing to be resilient in buffering wider negative landscape trends. 'Low PA' landscapes have had less positive impact than 'high PA' landscapes, despite contributing more to overall network representativeness, and will require conservation intervention to improve landscape resilience. The English Nature Recovery Network and similar initiatives in the other countries of GB provide opportunities to tackle this, through implementing landscape-scale restoration approaches in a systematic way.

For the last 40 years, only landscapes with high levels of protection or topographic variation have had a significant positive effect on achieving long-term conservation outcomes, and this should be considered within future conservation plans. Long-term monitoring for the entire network continues to be important in facilitating further investigation into network effectiveness and to learn from past network performance. SCP would have improved the GB network had it been used through improving initial PA network representativeness, and to a lesser extent resilience, and it thus would be a valuable tool in improving future conservation planning.

CRediT authorship contribution statement

CAC: Conceptualisation, Methodology, Formal Analysis, Data Curation, Validation, Writing - Original Draft, Visualisation. CDT: Methodology, Writing - Review & Editing. MDM: Writing - Review & Editing. HQPC: Writing - Review & Editing, Funding acquisition. CMB: Conceptualisation, Methodology, Writing - Review & Editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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