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The benefits of protected areas for bird population trends may depend on their condition

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ABSTRACT

The Post-2020 Global Biodiversity Framework calls for at least 30% of land and sea to be protected by 2030. Whilst there is growing evidence that protected areas can benefit biodiversity, to achieve the greatest possible gains from their expansion, we must understand how protected area quality impacts upon biodiversity metrics. We used UK BTO/JNCC/RSPB Breeding Bird Survey data and protected areas condition data from national Common Standards Monitoring, to test whether improving site condition (for which there are UK policy targets) would contribute to stated policy targets to increase species' abundance. After controlling for differences in climate, land cover, and elevation, we found a positive association between the proportion of favourable habitat and bird abundance trends in the UK, while in Wales, Scotland and Northern Ireland combined, the positive effect was also significantly greater than in unfavourable habitat. Conversely, we also found a negative effect of proportion of favourable habitat on bird abundance. There was no evidence that these relationships varied between conservation status or many of the traits considered, although there was some evidence that favourable condition was beneficial for habitat specialists, cold-adapted species, and varied by habitat. Our findings suggest that improving the condition of protected areas currently in unfavourable condition, will contribute to nature recovery as measured by species' abundance trends in some circumstances. This also suggests that achieving the "30 by 30" target without ensuring those protected areas are of sufficient quality, may not be sufficient to restore biodiversity.

1. Introduction

The Anthropocene is characterised as the time in which humans have had significant impacts on the global environment, resulting in substantial biodiversity declines (Johnson et al., 2017). To reverse these trends, the United Nations Convention on Biological Diversity (CBD) pledged to increase the global network of land and sea that is protected from human pressures. The objective of Aichi target 11 was for at least 17% of the terrestrial earth and inland waters and 10% of oceans to be designated for protection by 2020 (UNEP, 2010). Although effective implementation has proved challenging, with huge variation between countries, overall, the 2020 Protected Planet Report showed major progress since 2010, with 16.6% of land and 7.7% of the world's oceans having protected status (an increase of 42%) (UNEP-WCMC and UNEP, 2021). Subsequently, a new Post-2020 Global Biodiversity Framework was established with an increased ambition for at least 30% of land and sea to be protected - and equitably managed for conservation - by 2030 (also referred to as "30 by 30") (CBD, 2020).

While the international community has made progress towards reaching its global target on protected area (PA) coverage, it is very far from achieving its commitments on the maintenance of these areas, with no explicit information on quality goals (UNEP-WCMC and UNEP, 2021). While many PAs are effective conservation measures, they vary in their aims, so simply designating them does not guarantee biodiversity protection (Geldmann et al., 2019). Key reasons for ineffectiveness include intensive farming practices, pollution, spread of non-native species (Bailey et al., 2022), or areas that are simply too small (Gardner et al., 2023). In some parts of the world, the human pressure within

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PAs has even increased compared to matched non-PAs (Geldmann et al., 2019). The level of benefit afforded to wildlife populations in PAs thus varies considerably (Coetzee et al., 2014). National and international conservation schemes to increase the number of PAs may be limited in their effectiveness and overestimate global progress to reduce biodiversity losses. Hence, several recent studies have cautioned against the hurried creation of new PAs, without also addressing the conditions required to enable their success (Geldmann et al., 2019; Bailey et al., 2022). Despite this recognition, research focused on understanding the significance of PA quality on biodiversity remains relatively sparse.

Current estimates by the UK government reports that 28% of UK land area is protected (Bailey et al., 2022), thus at face value, it appears that the UK is on track to achieving the proposed 2030 Global Biodiversity Framework target of 30% protected land and seas (CBD, 2020). However, only 11.4% is designated primarily for nature conservation, as defined by Special Areas of Conservation (SACs) and Special Protected Areas (SPAs), established by European Legislation in 1979, and Sites of Special Scientific Interest (SSSIs) designated under national legislation in 1981. There is clear cross-taxa evidence that PAs contain more species than equivalent unprotected sites in the UK, and more rare species (Barnes et al., 2023; Cooke et al., 2023), indicating that the benefits of the protected area network may be greatest for species of conservation concern. However, current condition monitoring of UK PAs, based on a range of ecological features, indicates that many are in poor condition (Fig. S1); the percentage of PAs evaluated as being in “favourable condition” in March 2020, was 50.2% for SSSIs (ASSIs in Northern Ireland), 42.8% for SACs and 51.2% for SPAs (Barnes et al., 2023). The percentage reported as being in “unfavourable recovering condition” was 34.5% for SSSIs, 30.8% for SACs and 27.0% for SPAs. The most conservative assessment suggests that as little as 4.9% of UK land area could be considered effectively protected when only strictly protected areas in favourable condition are included (as defined by the IUCN Protected Area Management Categories Ia-IV, where nature conservation must be the main management objective (Starnes et al., 2021; Dudley, 2008)). However, little progress has been made towards assessing the effectiveness of protected area management in contributing to the recovery of biodiversity (Buchanan et al., 2020), or their impacts on surrounding areas from spillover (where the benefits of protection extend beyond the boundaries of PAs) (Shen et al., 2022) or the unintended effects from leakage (land-use change displaced to outside the PA) (Fuller et al., 2019). Studies undertaken have largely been restricted to a single habitat (e.g. forests (Shen et al., 2022; Fuller et al., 2019)), marine habitats (Di Lorenzo et al., 2020; Lenihan et al., 2021) or a subset of biodiversity indicators (Geldmann et al., 2013; Watson et al., 2014).

Assessing the condition of sites is not easy, particularly with respect to biodiversity. Condition may vary for different species along an ecological or management gradient making it difficult to measure and to generalise. In the UK, our best measure of PA condition comes from data collected by Statutory Nature Conservation Bodies (SNCBs) in each country. They are responsible for monitoring the status of SSSIs, SPAs and SACs in the four component countries of the UK (England, Northern Ireland, Scotland and Wales), by independently assessing PA condition with respect to standardised ecological characteristics.

One approach to evaluating the importance of conservation management in PAs has been to use long-term, large-scale citizen science datasets of bird counts (Sanderson et al., 2023). Such analyses have shown that the restoration and management of lowland wet grassland can have positive effects on the population trends of four wader species of conservation concern (Jellesmark et al., 2021). A comprehensive analysis of PA performance in the UK found strong evidence that they increase the occurrence and abundance of bird species, with benefits being greatest for species of highest conservation concern (Barnes et al., 2023). This study did not assess PA condition but found that although bird productivity (breeding success) was not improved within PAs across the species considered, there was a positive relationship between the effect of PAs on productivity, and the effect of PAs on species abundance. This strongly signifies that habitat quality and associated density-dependent limitations may be important mechanisms underpinning observed relationships between PA extent and biodiversity trends. Therefore, when assessing whether a country is meeting its biodiversity targets and reversing the loss of biodiversity, it is not just the size and quantity of PA that is likely to be important, but also their management and condition of sites (Gardner et al., 2023; Buchanan et al., 2020; Wauchope et al., 2022). This may alter a country’s position from appearing to meet the targets, to failing to meet them by a substantial margin (Starnes et al., 2021).

Given stated policies within UK countries to restore 75% of protected sites to favourable condition by 2042 (The Office for Environmental Protection, 2023), we particularly want to understand whether delivering on this target will also contribute to another stated biodiversity policy target to stabilise long-term biodiversity trends by 2030, and increase species populations by 10% by 2042 (The Office for Environmental Protection, 2021). We investigate this by linking long-term breeding bird survey data, previously used to identify positive impacts of PA extent (Barnes et al., 2023), with PA condition data. Firstly, we hypothesize that PA sites in favourable condition will have higher bird abundances than PA sites in unfavourable condition, although this could be due to spatial coincidence in site condition and abundance rather than a causal link. Secondly, we hypothesize that PAs in favourable condition will likewise support higher abundance trends than those in unfavourable condition. This second test would provide stronger evidence for their being a mechanistic link between long-term biodiversity trend and site condition. Thirdly, we also predict that species of highest conservation concern will be the species’ most positively associated with favourable site condition, since they are often dependent on rarer, protected habitats (Barnes et al., 2023).

2. Methods

To assess how PA condition affects bird abundance and trends in abundance, we used condition data provided by the statutory nature conservation bodies (Natural England, Natural Resources Wales, Northern Ireland Environment Agency and NatureScot), combined with extensive bird population data from the BTO/JNCC/RSPB Breeding Bird Survey (BBS). The condition data is referenced to the whole PA region (SSSI/ASSI, SAC or SPA), while the BBS data is per 1-km grid square, so we were required to spatially match the two datasets (described in the “Analysis” section below).

2.1. Condition data collection

The condition data was collected as part of a Common Standards Monitoring (CSM) programme initiated in 1998, to assess the results of management action and conservation policy. Condition was evaluated against agreed standards on a 6-year reporting cycle, using ecological interest features (habitats, species or geology) for which the PAs have been designated – i.e. in accordance with SSSI/ASSI selection guidelines (JNCC, 2003). For example, for habitats they might be heathland or woodland, for species they might be butterflies or breeding birds, and geological features might be fossils or landforms. For each feature, performance indicators are developed by identifying the key attributes which describe its condition (e.g. habitat extent or quality, species population size or distribution). Each attribute is measured and compared to the set target value, and the feature of interest is then identified as being in one of the following categories: *i)* Favourable – maintained, *ii)* Favourable – recovered, *iii)* Favourable - declining, *iv)* Unfavourable – recovering, *v)* Unfavourable - no change, *vi)* Unfavourable – declining. PA sites may have multiple features of interest, and each is assessed separately. Condition assessments are usually made during a structured walk across each site, but sometimes other information is used (e.g. aerial photographs, satellite imagery). For Northern Ireland, Wales and Scotland, each PA is ascribed multiple whole-feature condition assessments, whereas for England, the data is not reported in relation to whole features across a PA. Instead, it is summarised across PA *units* (originally divided by tenure), whereby the individual assessments of each 'unit-feature' are combined into a single category to represent the overall condition of each unit within the PA using the least favourable business rule (i.e. the lowest condition of any of the features within that unit - for example if grassland was favourable but woodland was unfavourable the unit would be categorised as unfavourable). Therefore, in contrast to the other countries, the condition of each feature in England is not assessed at the scale of individual features. This means that England condition assessments are less likely to reflect overall condition of the protected site as measured across multiple features.

2.2. Bird data collection

The BBS is an annual citizen science scheme supported by a partnership of BTO, JNCC and RSPB to monitor the abundance of breeding birds across the UK since 1994. It consists of randomly located 1-km squares, chosen regionally by stratified random sampling so that multiple habitat types are covered with a greater number of squares occurring in areas with more surveyors (Harris et al., 2022). Two visits are made to each square in the breeding season, one early in April to mid-May, and one late from mid-May to June. Surveyors record all adult birds encountered while walking two 1-km line transects across each square. The random selection of BBS squares means they can occur in any type of habitat. Therefore, the habitat along the transect lines is also recorded using a hierarchical system comprising of nine broad categories, for each 200 m section (Crick, 1992). Our square-level measure of annual abundance was derived from the maximum count of each species from the two visits to each square per year, as used widely in previous analyses (Barnes et al., 2023; Sanderson et al., 2023; Morrison et al., 2021).

2.3. Analysis

We used the same initial dataset as used by Barnes et al. (Coetzee et al., 2014) (which excludes non-breeding birds and large flocks), however, only those BBS squares which overlapped a PA were included in this analysis. To match PA condition with BBS data, we first obtained shapefiles for the geographic extent of every PA from the Natural England Open Data Geoportal (naturalengland-defra.opendata.arcgis.com), Scottish spatial data portal (spatialdata.gov.scot/geonetwork/srv/eng/catalog.search), Welsh Lle Geo-portal (lle.gov.wales/catalog) and Open Data NI (www.opendatani.gov.uk). Likewise, we obtained shapefiles of every 1-km BBS square from BTO Trends 2022 (Harris et al., 2022) in all UK countries. All shapefile data were transformed into the British National Grid projection. We then used the "st_intersection" function in the 'sf' package in R (v1.4.1717) (Edzer, 2018; Pebesma and Bivand, 2023) to match the shapefiles and calculate the area of overlap of the three PA types (SSSI/ASSI, SAC, SPA) within each BBS square. We merged the shapefiles with the condition data by PA identity, and corrected any non-matches (e.g. spelling discrepancies). Due to differences in sampling and assessment protocols between countries, and to ensure adequate sample sizes, we pooled all condition assessments as being either in a desired state (i.e. favourable; categories (*i*)-(*iii*) above) or not having attained the desired state (i.e. unfavourable; categories (*iv*)-(*vi*) above) and removed all features where the condition was not assessed. Multiple assessments were made across different years for most features, but the timeframe over which any changes in assessment should operate was not clear. They could reflect changes that occurred between two assessment periods, which were of varying length apart, but it was also not clear how quickly any changes in assessment might be expected to impact bird populations (if at all). For this reason, the analysis focussed on spatial variation in site condition assessment on variation in bird abundance and trend and did not consider the effects of changes in site condition assessment through time. However, to test the extent to which the period of assessment altered the results, we firstly used the most recent condition assessment for each feature type, and subsequently, repeated our analyses using the earliest condition assessment for each feature type, as two potential alternative approaches to summarising spatial variation in site condition (Table S1 shows the number of PA features [or units in the case of England] that changed condition between the two assessment periods for each country).

Due to the multiplicity of feature assessments, we created variables that reflected the average condition of each PA that contained an overlapping BBS square. The number of feature assessments per PA was highly variable (range = 1–266, mean = 7.3) and was found to relate to land cover type e.g. beaches and sand dunes had few features, while moors and heathland had many (Fig. S1). We therefore developed a method to obtain two values defining the extent of PA in favourable condition F_b and in unfavourable condition U_b within the BBS square b, by summing the product of: (1) the proportion of favourable (for F_b) or unfavourable (for U_b) features, out of the total number of assessed features, for each PA i that intersects the BBS square, and (2) the area of intersection $area_{i,b}$ between the PA and the BBS square, according to the following equations:

$$F_b = \sum_{i=1}^{I} \frac{N\ favourable_{i,b}}{N\ total_{i,b}}\ area_{i,b}$$

$$U_b = \sum_{i=1}^{I} \frac{N\ unfavourable_{i,b}}{N\ total_{i,b}}\ area_{i,b}$$

where *N favourable* (or *N unfavourable*) is the number of features that have favourable (or unfavourable) condition in the PA intersecting the BBS square, *N total* is the total number of assessed features and *area* is the area in m^2 of the intersection of each PA and BBS square. If multiple PAs were overlapping within the same BBS square, the portion of area in each PA that was overlapping other PAs was divided by the number of overlapping PAs, so that the sum of all $area_{i,b}$ over each BBS square b was equal to the area of the union of all PAs intersecting the square (which is never greater than $1km^2$).

The proportions of features of a protected area that are unfavourable and favourable are perfectly inversely correlated, but our equation also takes account of the land cover of the PA within each grid cell. Essentially, we have created two variables that reflect the land cover of favourable PA and the land cover of unfavourable PA. The same grid cell cannot have high cover of both favourable and unfavourable PA since land area is finite, but the same grid cell can have low cover of both favourable and unfavourable, or low of one and high of the other. This explains the low correlation between the two condition land covers (corr. coeff = 0.14; Fig. S2).

No spatial information was available on the extent of individual features for any of the countries, and so it was not possible to measure the extent of favourable or unfavourable features more precisely. Note, as the data on PA condition in England was not collected by features but summarised by PA management unit, the condition assigned to each unit was either entirely favourable or entirely unfavourable, unlike the other countries where condition was expressed in proportion to all the feature assessments. We framed our analysis to explicitly ask whether unfavourable PAs have a positive effect on abundance trends or whether only favourable PAs do, by modelling two condition-related predictor variables. We therefore tested whether the effect of favourable PA cover (F_b) differs from that of unfavourable PA cover (U_b), and separately, whether the effects of both favourable (F_b) and unfavourable (U_b) PA cover differs from zero.

2.4. Modelling biodiversity metrics

We use the model to compare the importance of favourable PA cover over unfavourable PA cover. In total, 1366 1-km BBS squares with condition scores contained data on 112 BBS species (using only native species and a threshold of >2500 records per species, which is c. 100 per year over the 25-year BBS period). This is a figure far lower than overall BBS coverage as many sites do not also contain protected areas and were therefore excluded from the analysis. We modelled bird abundance as functions of overall area of favourable condition F_b and overall area of unfavourable condition U_b using Bayesian generalized linear models (BRMs) with default priors, comprising negative binomial distributions (and log link functions) in the 'brms' package in R (v4.2.2) (Wood, 2017; Bürkner, 2017). We used a two-way interaction between F_b or U_b and year, to test for the effect of PA condition on population size (the main effect of each condition term) and trend (the interaction term with year) within the same model:

$$\log\left(\frac{C_{by}}{Nsquares_b}\right) = \left(F_b \times y\right) + \left(U_b \times y\right) + F_b + U_b + y + y^2 + habitat_b + f(easting_b, northing_b, elevation_b) + 1|ycat_y + 1|PA_b$$

where C_{by} is the expected count in the BBS square b in year y (year is a numerical variable, centred and divided by 2 standard deviations); F_b and U_b are the extent of PA in favourable or unfavourable condition as defined above; $habitat_b$ is a categorical variable describing the broad habitat category (Barnes et al., 2023); f is a tensor smooth function to account for variation in climate and other landscape-scale conditions across the UK; $ycat_y$ and PA_b are year as a categorical variable, and PA identity, respectively, included as random effects to account for weather and pseudoreplication of PA condition (where PAs intersect multiple BBS squares); $Nsquares_b$ is an offset that accounts for the number of squares that contribute to the count (usually 1, but may be 2 in poorly covered upland areas where an adjacent BBS square is often added to maximise sampling – and in such cases the counts are summed across the 2 squares (Harris et al., 2022)).

Due to the different methods of assessing PA condition across countries – namely, the greater uncertainty of the extent to which the English condition assessments represent condition across the features of a protected site – we fitted separate BRMs for *i*) the UK, *ii*) Northern Ireland, Scotland and Wales combined (NI/WA/SC) and *iii*) England only (ENG). The combined NI/WA/SC dataset included 383 1-km BBS squares, compared to ENG only which totalled 992 1-km BBS squares – with ENG therefore contributing much more to the UK-wide analysis. For some species, the initial BRMs failed to converge, due to having no associations with certain habitat types in the model. Therefore, we removed any such explanatory variables before running the model again for these species. Using the earliest condition assessments which coincided with the BBS data, we were able to model 110 species for the UK, 70 for NI/WA/SC and 101 for ENG. For the latest condition assessments which coincided with the BBS data, we modelled 112 species for the UK, 69 for NI/WA/SC and 102 for ENG. To compare the mean species coefficients from the BRMs for each population metric (abundance and abundance trends), all the effect estimates were weighted by the inverse of the square of their standard error to give less weighting to those species for which the effect of favourable or unfavourable PA extent was estimated with less confidence. We capped the weightings to the median standard error of the condition effect coefficient, to prevent common species with extremely low SEs from having very high weights. We used Chi-squared tests to compare the proportions of species with significantly positive verses significantly negative coefficients.

2.5. Traits analysis

To test the hypothesis that favourable PA condition will benefit the same species that have been found to benefit from PAs in general (i.e. rare, specialist and cold adapted species, those of high conservation concern and those of certain habitats – building on previous work (Barnes et al., 2023)), we fitted linear models using the PA condition effect coefficient for each species from the main analysis as our response variable and two different categories of traits as the explanatory variables: *i*) species conservation status, and *ii*) a suit of 12 ecological traits. Species status was defined using the Birds of Conservation Concern (BoCC) designations (Gibbons et al., 1996), which categorizes species according to the vulnerability of their populations: Green (least concern), Amber (moderate concern), and Red (highest concern). The ecological traits we explored were: *i*) log mean body mass (Robinson, 2005), *ii*) log population size (from the Avian Population Estimates Panel in the 1990s (Stone et al., 1997) and 2010s (Woodward et al., 2020)), *iii*) log population change (log of ratio between the population size in the 2010s and 1990s), *iv*) species specialisation index, SSI (degree of habitat specialisation, derived from the variation in species density across 12 dominant habitat types and all BBS squares (Sullivan et al., 2016)), *v*) species temperature association, assessed by the species temperature index, STI (average temperature over the species full European breeding range (Devictor et al., 2012)) and *vi*) habitat status (primary habitat of each species (Gibbons et al., 1993)). To account for relatedness between species in the ecological trait models, we performed a phylogenetically weighted regression using a Markov chain Monte Carlo Sampler (MCMC) and generalized linear mixed model from the 'MCMCglmm' and 'ape' packages in R (v4.2.2) (Hadfield, 2010; Paradis and Schliep, 2019). We used the same Ericson phylogenetic tree averaged from 1000 trees, as per the previous paper on PA extent (Barnes et al., 2023) (originally downloaded from birdtree.org (Jetz et al., 2012) accessed 8 March 2021), and ran a single chain simulation with 50,000 iterations.

For both the species status and ecological traits analysis, we fitted 4 separate linear models for: (*i*) the abundance (main effects) coefficients of favourable PA condition; (*ii*) the abundance coefficients of unfavourable PA condition; (*iii*) the abundance trend (interactive effect with year) coefficients for favourable PA condition and (*iv*) the abundance trend coefficients for unfavourable PA condition. We present the species conservation status for each country grouping above, whereas for the ecological traits analysis we only show the results for the whole UK to avoid models with small sample sizes. To compare the species-specific effect estimates from the BRMs for each population metric (abundance and abundance trends), all of the effect estimates were weighted by the inverse of the square of their standard error to give less weighting to those species that were estimated with less confidence - we again capped the weightings to the median standard error of the condition effect coefficient (Lee et al., 2011). For the species conservation status and ecological traits analyses, we performed checks for correlation between the explanatory variables and found that all cross-comparisons were well below $r = 0.7$ (Dormann et al., 2013). We checked the $\widehat{R}$ values from the BRMs output for each species model, to ensure that inferences were only drawn from converged models.

3. Results

We ran the BRMs separately for each species, and to summarise the models for each geographic grouping we took the average coefficient across all species, but we also looked at the proportion of species with positive and negative effects. The results for the earliest and latest condition assessment periods were similar, and since we are most interested in the current situation, from here on we only report the results for the latest assessments. We plot the model summaries for the latest PA condition assessment period in Fig. 1 (but show the earliest PA condition assessment period in Fig. S3).

3.1. Effects of PA condition on species' abundance

For the UK overall, and across all species, the extent of PA in favourable condition had a significant negative mean effect on species abundance (mean slope = −0.19; 95% CIs, [−0.33, −0.05]; $t_{(111)} =$

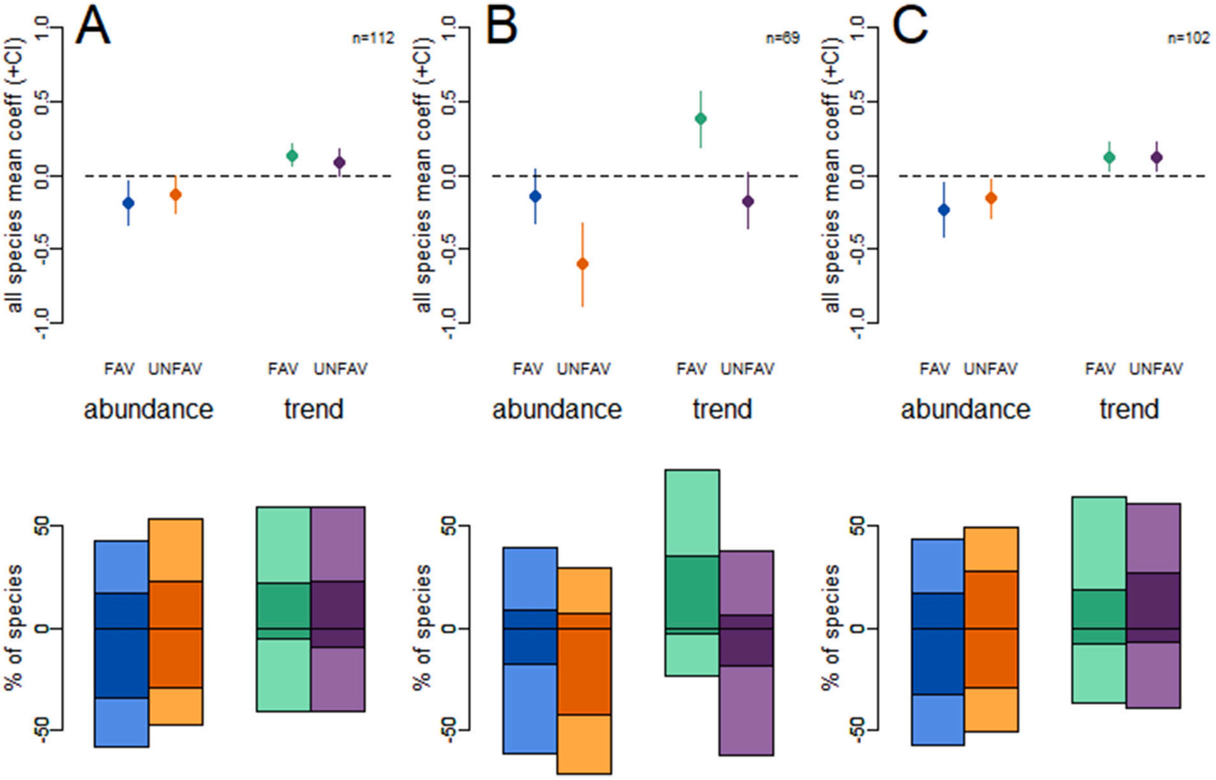

Fig. 1. Summarising the effect of PA condition on abundance and trend dynamics of UK breeding bird species. Uses condition data from the latest assessments coinciding with the BBS data (we did not include assessments made in 2023), for A) the whole UK (1st column), B) Northern Ireland, Wales and Scotland combined (2nd column) and C) England only (3rd column). The point plots represent the means (±95% CIs) of all modelled species with negative and positive associations between the population measure (abundance and trend in abundance) and favourable or unfavourable PA condition (weighted by area that intersects the monitored 1-km square). The bar graphs represent the percentage of species with a significant (bold colours) or non-significant (pale colours) relationship with PA condition.

2.59, $p = 0.01$), and likewise for the extent of PA in unfavourable condition (mean slope = −0.13; 95% CIs, [−0.26, 0.00]; $t_{(111)} = 2.00$, $p = 0.05$). Comparing the proportions of species with positive versus negative associations showed that more species had a negative association with favourable PA extent (17% positive vs 34% negative; $\chi^2 = 5.68$, $p = 0.02$), but there were no significant differences in the proportions for unfavourable PA extent (22% positive vs 30% negative; $\chi^2 = 0.85$, $p = 0.36$; Fig. 1A, Table S2). The results for NI/WA/SC showed that the extent of PA in favourable condition had no significant mean effect on species abundance (mean slope = −0.15; 95% CIs, [−0.33, 0.04]; $t_{(68)} = 1.58$, $p = 0.11$), whereas the extent of PA in unfavourable condition had a mean negative effect (mean slope = −0.60; 95% CIs, [−0.88, −0.32]; $t_{(68)} = 4.26$, $p << 0.001$). More species had negative associations with unfavourable PA extent (7% positive vs 42% negative; $\chi^2 = 15.6$, $p << 0.001$) but not favourable PA extent (9% positive vs 17% negative; $\chi^2 = 1.39$, $p = 0.24$; Fig. 1B, Table S2). The mean results for ENG showed that the extent of PA in favourable condition had a significant negative mean effect on species abundance (mean slope = −0.23; 95% CIs, [−0.42, −0.05]; $t_{(101)} = 2.46$, $p = 0.01$), and likewise the extent of PA in unfavourable condition (mean slope = −0.16; 95% CIs, [−0.29, −0.02]; $t_{(101)} = 2.30$, $p = 0.02$). More species had negative association with favourable PA extent (17% positive vs 32% negative; $\chi^2 = 4.50$, $p = 0.03$) but not unfavourable PA extent (28% positive vs 29% negative; $\chi^2 = 0.02$, $p = 0.90$; Fig. 1C, Table S2). Our first hypothesis – that sites in favourable condition will have higher species' abundance on average than unfavourable sites – is only partially supported by the data for Northern Ireland, Wales and Scotland combined, and not apparent in England, or across the UK for which the English data form the majority.

3.2. *Effects of PA condition on abundance trends*

For the UK overall, the extent of PA in favourable condition had a significant positive mean effect on species trends (mean slope = 0.14; 95% CIs, [0.06, 0.21]; $t_{(111)} = 3.57$, $p < 0.001$), while the extent of PA in unfavourable condition had no significant effect (mean slope = 0.08; 95% CIs, [−0.01, 0.17]; $t_{(111)} = 1.83$, $p = 0.07$). More species had positive associations with favourable PA extent (21% positive vs 5% negative; $\chi^2 = 9.63$, $p = 0.001$), and unfavourable PA extent (22% positive vs 10% negative; $\chi^2 = 4.69$, $p = 0.03$; Fig. 1, Table S2). The results for NI/WA/SC showed that the extent of PA in favourable condition had a significant positive mean effect on species trends (mean slope = 0.38; 95% CIs, [0.19, 0.57]; $t_{(68)} = 3.86$, $p < <0.001$), while PA in unfavourable condition had no significant effect (mean slope = −0.17; 95% CIs, [−0.36, 0.02]; $t_{(68)} = 1.77$, $p = 0.08$). More species had positive associations with favourable PA extent (35% positive vs 3% negative; $\chi^2 = 16.7$, $p << 0.001$; Fig. 1B, Table S2) and negative associations with unfavourable PA extent (6% positive vs 19% negative; $\chi^2 = 3.76$, $p = 0.05$; Fig. 1, Table S2). The mean results for ENG showed that the extent of PA in favourable condition had a significant positive effect on species trends (mean slope = 0.12; 95% CIs, [0.03, 0.22]; $t_{(101)} = 2.52$, $p = 0.01$), and likewise the extent of PA in unfavourable condition (mean slope = 0.12; 95% CIs, [0.03, 0.22]; $t_{(101)} = 2.52$, $p = 0.01$). As in the UK-wide analyses, more species had positive associations with favourable PA extent (19% positive vs 8% negative; $\chi^2 = 3.70$, $p = 0.05$) and unfavourable PA extent (27% positive vs 7% negative; $\chi^2 = 10.6$, $p = 0.001$; Fig. 1C, Table S2).

To supplement the above analysis, we also explicitly tested the differences in the effect sizes of favourable PA condition and unfavourable PA condition for both abundance and abundance trend. For NI/WA/SC, the effect size on trends for PAs in favourable condition was significantly greater (i.e., more positive) than the effect size for PAs in unfavourable condition ($t_{(68)} = 3.33$, $p = 0.0014$). While the effect size on abundance for PAs in unfavourable condition was significantly lower (i.e., more negative) than the effect size for PAs in favourable condition ($t_{(68)} = 2.76$, $p = 0.007$). In addition, for NI/WA/SC the proportion of species with negative abundances was significantly greater in unfavourable PAs compared to favourable PAs (42% unfav vs 17% fav; $\chi^2 = 6.24$, $p = 0.01$; Fig. 1B). Whereas the proportion of species with positive abundance trends was significantly greater in favourable PAs compared to unfavourable PAs (35% fav vs 6% unfav; $\chi^2 = 12.9$, $p << 0.001$; Fig. 1B), while the proportion of species with negative abundance trends was significantly greater in unfavourable PAs compared to favourable PAs (19% unfav vs 3% fav; $\chi^2 = 6.67$, $p = 0.04$; Fig. 1B). None of the other contrasts were statistically significant (Table S3). Our results therefore partially support our second hypothesis - that species in PAs with favourable condition will have more positive abundance trends than if those PAs are in unfavourable condition. This was apparent in the data for Northern Ireland, Wales and Scotland combined, but not apparent in England, and therefore also not apparent across the UK.

3.3. *Variation in species' responses to PA condition*

Overall, species status had no significant impact upon the response of species to PA condition for either the UK, NI/WA/SC or ENG (Fig. 2, Table S4). However, there was some evidence that the abundance trends of Red listed species in the UK were more positively associated with both favourable and unfavourable PA extent (fav coeff = 0.22; 95% CIs, [0.07, 0.38]; unfav coeff = 0.26; 95% CIs, [0.08, 0.44]), and likewise for ENG (fav coeff = 0.22; 95% CIs, [0.02, 0.43]; unfav coeff = 0.40; 95% CIs, [0.21, 0.60]). In NI/WA/SC the abundance of Green listed species was negatively associated with unfavourable PA extent (coeff = −0.82; 95% CIs, [−1.21, −0.42]) while the abundance trends were positively associated with favourable PA extent (coeff =0.51; 95% CIs, [0.22, 0.79]). The abundance of Red listed species also had negative associations with unfavourable PA extent (coeff = −0.69; 95% CIs, [−1.31, −0.07]). When comparing favourable and unfavourable PA extent, more species in NI/WA/SC with Green or Red status had negative abundances in unfavourable PAs than compared to favourable PAs (Green coeff = −0.50; 95% CIs, [−0.97, −0.02]; $p = 0.04$; Red coeff = −1.69; 95% CIs, [−2.90, −0.48]; $p = 0.01$; Fig. 2, Table S5). For abundance trends, more species in NI/WA/SC with Green status had positive associations in favourable PAs than compared to unfavourable PAs (coeff = −1.13; 95% CIs, [−1.54, −0.70]; $p << 0.001$), and likewise for Amber species (coeff = −0.68; 95% CIs, [−1.24, −0.12]; $p = 0.02$), but not for red species though they did tend towards the positive in favourable PAs. Hence, our third hypothesis – that species of the highest conservation concern will be the species most positively associated with favourable site condition – was partly supported, since we found evidence of more positive responses for favourable as well as unfavourable PA condition in Red listed species in the English and all UK data.

For the wider analyses of ecological traits, we were only able to consider the UK dataset because of sample size (Figs. 3, S4; Tables S5, S6). Habitat specialism and urban species were the only traits associated with an effect of favourable PA condition. Specifically, we found that habitat specialism (assessed by SSI), was positively associated with the effect of favourable PA condition on abundance (coeff = 0.87; 95% CIs, [0.27, 1.41]), indicating that specialists were more likely to associate with protected sites in favourable condition than generalists. Urban species were negatively associated with the effect of favourable PA condition on abundance (coeff = −0.76; 95% CIs, [−1.48, −0.06]). For the remaining traits, we tended to find associations with the extent of protected sites in unfavourable condition. Temperature preference (STI) was negatively associated with the effect of unfavourable PA condition on trends (coeff = −0.39; 95% CIs, [−0.68, −0.12]), meaning that warm-adapted species were more negatively affected by unfavourable conditions than cold-adapted species. Mass was negatively associated with the effect of unfavourable PA condition on abundance (coeff = −0.38; 95% CIs, [−0.73, −0.01]) and trends (coeff = −0.37; 95% CIs, [−0.68, −0.12]), meaning that larger birds were more negatively affected by unfavourable conditions. Population size was negatively associated with the effect of unfavourable PA condition on abundance (coeff = −0.69; 95% CIs, [−1.02, −0.37]), suggesting that species with larger populations were more negatively affected by unfavourable conditions. Likewise, population change was negatively associated with the effect of unfavourable PA condition on abundance (coeff = −0.37; 95% CIs, [−0.63, −0.08]), suggesting that species with more positive trends were more negatively affected by unfavourable conditions. Turning to habitat association, wetland species showed a more positive effect of unfavourable PA condition on trends (coeff = 0.78; 95% CIs, [0.40, 1.17]) than species using other habitats. When comparing the effects of favourable PA condition versus unfavourable PA condition for each categorical trait (7 habitats), using weighted *t*-tests, no significant results were found for the UK (Table S5). Overall, we provide some support for the findings of the previous paper (Buchanan et al., 2020) regarding the species which benefit most from PAs, since our results show that favourable PA condition promotes habitat specialists, cold adapted species (i.e. they experience a less negative effect of unfavourable condition), and those associated with certain habitats.

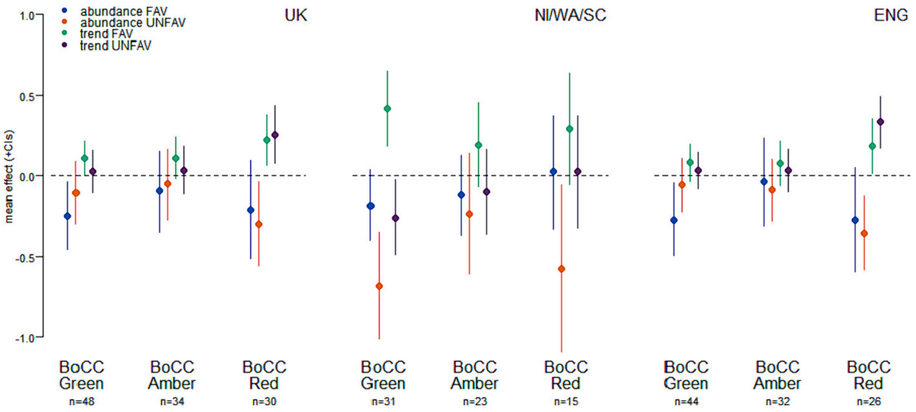

Fig. 2. How the effect of PA condition on population measures varies with species conservation status. The mean (±95% CIs) relationship between PA condition and abundance and trend dynamics in relation to species population vulnerability (Bird of Conservation Concern, BoCC; Green = least concern, Amber = moderate, Red = highest concern) for the whole UK (UK), Northern Ireland, Wales and Scotland combined (NI/WA/SC), and England (ENG) only. The horizontal dashed line is the line of no effect. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

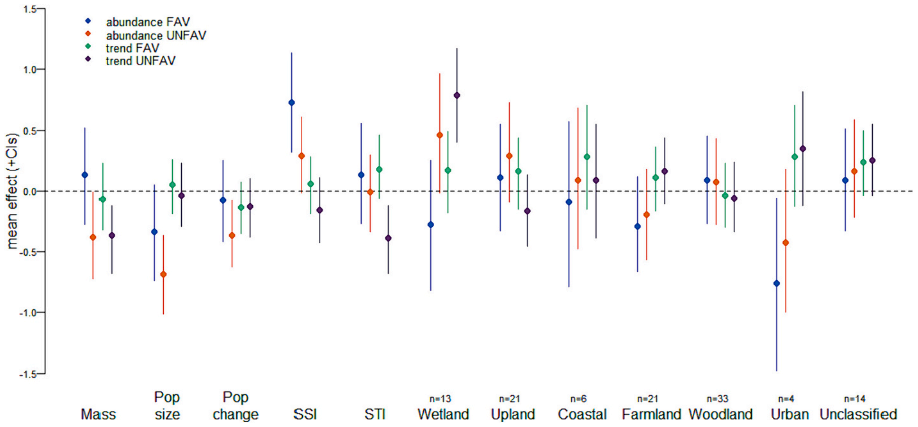

Fig. 3. How the effect of PA condition on population measures varies with species ecological traits for the whole UK. The mean (±95% CIs) relationship between PA condition and abundance and trend dynamics in relation to various species traits from a phylogenetically weighted regression. Species traits include; log-transformed values of mass, population size and population change; Species Specialisation Index (SSI) and Species Temperature Index (STI), and the 7 habitat types in which species are most commonly found. The horizontal dashed line is the line of no effect.

4. Discussion

The positive impacts of PAs on bird population trends in the UK, particularly for habitat specialists, rare, and declining species have been previously demonstrated (Geldmann et al., 2013; Watson et al., 2014), but the benefit of PAs varied between designation types – being greatest for SPAs specifically targeted towards bird conservation (Barnes et al., 2023). Given that many of these PAs are currently regarded as being in unfavourable condition in the UK, and the stated ambition of restoring 75% of them to favourable condition by 2042 (The Office for Environmental Protection, 2023), we aimed to understand how PA condition affects biodiversity (bird) trends. In other words, what contribution can improving PA condition make to improving biodiversity population trends? Our study compared the effect estimates of our condition scores (extent of PA in favourable condition and extent of PA in unfavourable condition) upon bird abundance and abundance trends. Although there was no evidence for a link between PA condition and bird abundance, we did find that trends in bird abundance were positively associated with the quality of protected areas as measured by PA condition across Northern Ireland, Scotland, and Wales, but not in England or across the UK. This is likely due to the different process for reporting and summarising site condition assessment in England compared to the other countries, that also would have strongly influenced the UK-wide analysis (since their relative contribution was almost 3 times greater). Condition in England was assigned by giving each PA unit the lowest condition of all the assessed features for that unit, thereby ignoring all features in favourable condition for any unit comprising at least one unfavourable feature and potentially downgrading its true condition. Nonetheless, the fact that our model found significant effects implies there is meaningful variation along the range of assessed condition scores within the 1-km BBS squares.

Although mixed, these results provide some evidence that progress towards improving the condition of PAs and restoring degraded ecosystems could improve species' biodiversity trends and consequently reduce extinction risk, though the strength of this relationship is likely to vary with context. As an example of the likely magnitude of benefit associated with improving PA condition, we used our model coefficients from the NI/WA/SC analysis (latest condition assessments; Fig. 1B) of the mean effect across species, to predict what effect transforming 50% of PA sites in unfavourable condition to favourable condition would have on average bird population trends over the next 10 years. For each species we calculated the predicted change in abundance (the sum of the predicted counts in 2029 across all PAs, divided by the sum of the predicted counts in 2019 across all PAs). Assuming that improving condition would have an immediate effect across species – the result was a 7% increase in abundance relative to those sites remaining in unfavourable condition. Repeating the same exercise but without converting 50% of unfavourable to favourable, the median was +0.4%, so essentially, almost the entire 7% increase in 10 years is attributable to the transformation of unfavourable into favourable condition. Therefore, progressing towards the stated favourable condition target should also contribute towards another stated UK target – to stabilise long-term biodiversity trends by 2030 and increase populations by 10% by 2042 (The Office for Environmental Protection, 2021), particularly as condition is measured in Wales, Northern Ireland and Scotland. In the context of the Kunming-Montreal Global Biodiversity Framework (UNEP-CBD, 2022) – ensuring at least 30% of degraded ecosystems are under effective restoration (Target 2) and at least 30% of areas are effectively conserved and managed through PAs and other conservation measures (Target 3) – we thus corroborate the view that progress towards both targets will also address Target 4 – to stop human induced extinction of species and promote the recovery and conservation of threatened species. Given that for many PAs, improving condition will be with respect to features of habitat condition, this provides some support of their being a mechanistic link between site condition and improving population trends of species.

However, while the creation of PAs is the main way the CBD targets are being realised in Europe, it is important to note that other effective area-based conservation measures (OECMs) also play a crucial role, including sustainable fisheries and agriculture, sustainable forestry, and sustainable tourism, as well as renewable energy generation and improving energy efficiency (Dudley et al., 2018; Jonas et al., 2014; Agung et al., 2022). Hence, setting aside protected areas must go together with addressing anthropogenic activities outside of these areas, especially so as not to exacerbate unsustainable land management (Fuller et al., 2019), or we risk undermining the benefit of the areas which are protected.

While we found no evidence that PAs in favourable condition were associated with higher species' abundance – and in fact found that for NI/WA/SC combined, species abundance was negatively correlated with the extent of PA in favourable and unfavourable condition – this accords with other studies which found a negative effect of PAs on common species (Cooke et al., 2023). In our case, it may be a result of the BBS data inherently comprising species that are relatively common and widespread, and therefore are not necessarily the rarest or specialist species most dependent upon PAs (Geldmann et al., 2013; Watson et al., 2014). Likewise, the number of common species in the BBS data may be overrepresented (due to higher encounter rates and our threshold of requiring a species to have >2500 records) compared to rarer, specialist species whose populations benefit from favourable PAs (Barnes et al., 2023). It may also reflect a location bias, as PAs have higher representation in the north compared to the south, and particularly in the uplands where there is relatively low habitat diversity with lower bird abundances (Stratigos et al., 2023) (Fig. S1). Alternatively, it may be a discord between the PA condition data and the BBS data, in that many condition assessments were based on target (rare) species or habitats for which the site was designated for, while the BBS counts involve common species which fare better in the wider environment outside of PAs (e.g. in farmland or urban areas). Notably, Barnes et al. (Coetzee et al., 2014) – which is the most comparable study – did not find that common species abundance was negatively linked to PAs. An important distinction between the two studies is that the BBS coverage was much lower in this study (1366 1-km squares compared to 6718 1-km squares (Barnes et al., 2023)) and only included squares containing PA within them. It has previously been found that population increases on protected sites can also lead to increases in neighbouring areas of non-PAs (Sanderson et al., 2023). Hence, all the squares covered in this analysis may have been subject to this spillover effect (Shen et al., 2022), as well as other effects originating from the overall composition and structure of habitats in the surrounding area (Boesing et al., 2018), thereby diluting any benefits of favourable PA condition and lacking a true zero-baseline for comparison, which may explain the negative effect of PAs that we found. Spillover effects have been shown to be greater for larger and older protected areas, and for more mobile species (Di Lorenzo et al., 2020). Further analyses could explore whether the magnitude or distance-decay of spillover effects depend on protected area condition.

In the UK and England, Red listed species were found to benefit from both favourable and unfavourable PAs, suggesting that – in contrast with previous studies (Barnes et al., 2023; Cooke et al., 2023) – improving PA condition may be less important for the most threatened or rarest species. However, the previous study using BBS data modelled a greater number of species ($n = 133$ compared to $n = 112$ here) comprising of more rarities – which may have abundances that are more positive in PAs. Therefore, to ascertain whether this was an effect of species selection sensitivity, we ran the analysis from the previous paper with only our 112 species and found no differences in the mean abundances [K-S test; $D = 0.06$, $p = 0.98$] or the mean trends [K-S test; $D = 0.05$, $p = 1.00$]. We therefore conclude that rare species benefit from PAs whatever their condition, although the effects are likely to be context specific and best revealed through more detailed and targeted studies on individual species.

Unfavourable PA condition was found to have negative effects on warm-associated species, large species, and larger populations, and so we may infer that improving PA condition would most likely benefit warm-associated, large bodied species. We also found some evidence that progress towards improving PA condition may benefit habitat specialists and that the effect would vary between habitats. This is not surprising given likely variation between habitats in the nature of the relationship between site condition as measured by current reporting and ecological condition for birds. For instance, we found that unfavourable PAs had a more positive effect on abundance trends of wetland species compared with species of other habitats, implying that species in this habitat are less dependent on favourable condition, or survive just as well in non-PA areas. This could be driven by moderate changes in nutrient status which can lead to increases in vegetation and insect productivity, potentially benefitting associated bird populations, but may be negatively linked to site condition for oligotrophic wetlands (Pounder, 1976). Hence, there can be a complex relationship between site condition and bird populations; The majority of moorland and heathland habitats are in unfavourable condition (Fig. S1) and climate change is expected to reduce the abundance of many cold adapted species (Pearce-Higgins, 2010; Pearce-Higgins et al., 2017), however, bare peat (a feature of unfavourable condition on upland peatlands) provides an important habitat for breeding waders (Pearce-Higgins and Yalden, 2004), and conversely those same species also benefit from management to improve peatland condition through restoring peatland hydrology (Carroll et al., 2011; Carroll et al., 2015). Therefore, the benefits of maintaining PAs in favourable condition varies across species and habitat, so applying a broad, cross-species modelling approach will inevitably miss some of the more subtle responses.

One of the main limitations of the analysis concerned the condition data for England, and the different approach to site condition assessment compared to the other countries. The positive effects of favourable PA condition upon trends were less apparent in England, and we were unable to identify whether this was due to differences in how condition was assessed (hence, why we analysed England separately), differences in the nature of the protected sites between countries, or spatial differences in bird population trends which tend to be more negative in England than other countries of the UK (Massimino et al., 2015). Despite this uncertainty, the fact that we found such a strong link in one of our analyses suggests that in some circumstances, improving site condition can lead to population increases in the species that occur there. Indeed, there are a growing number of examples for the UK which suggest that management to improve the quality of PAs can have a positive impact on the conservation of rare and declining bird species, including breeding waders (Jellesmark et al., 2021; Pearce-Higgins et al., 2019). Where conservation management is likely to contribute to improvements in the condition of PAs – as measured by site condition assessment – then our analysis should identify that concordance. But where management for individual species does not necessarily contribute to improving the condition of PAs for other features of interest, then we are unlikely to detect this. Clearly the extent to which there is an association between improving PA condition for reasons of habitat restoration and species' population trends will be context dependent. If management is targeted at individual species it will most likely contribute positively to the recovery of those species, but more general restoration of PA condition may still benefit many species (Bowgen et al., 2022). Finding stronger links between condition and trends would require much more detailed and tailored analysis, with information on the habitat composition of each PA, which was not available.

Furthermore, since condition is assessed for different types of features (habitat, species, and geology) the effects are likely to co-vary, and in the case of geological features their effects may not be similar, i.e. the impact of geological features being in unfavourable condition may differ from the impact of habitat being unfavourable. However, there were very few geological feature assessments (<5 % of all assessments) so any potential noise in the analysis from unimportant features should be minimal. In addition, unlike the BBS data, the condition data was not assessed annually, and because of the variation in reporting periods and uncertainty over any lag between changes in site condition and bird populations, we used the earliest and most recent assessment only as two potential alternative descriptions of condition. This meant that we could not investigate how changing condition, or habitat degradation through time is affecting bird population metrics, and for some sites the most recent assessments were over a decade old. While these monitoring timescales are sufficient and appropriate for reporting changes in site condition for policy targets, more detailed reporting and understanding of changes in the condition of protected sites – particularly regarding key ecological measures affecting bird species such as hydrology and structure – would greatly increase the potential to inform the recovery of PAs and maximise the benefits for the species within them. Such analysis could also take account of how bird populations outside of PAs may be affected by habitat condition.

5. Conclusions

Despite the relatively coarse nature of the PA condition data, and the complexities of the analysis, we have provided high-level evidence that PA condition is linked to long-term bird population trends in at least some circumstances. Importantly, this means that conservation action to restore and improve the condition of sites may make as much or more of a contribution to restoring biodiversity loss as expanding the PA network. This provides the potential for win-win solutions for multiple policy objectives, both for governments in the UK and with respect to the CBD framework (i.e. targets 2 and 3 of the Kunming-Montreal Global Biodiversity Framework). Where appropriate management is implemented, PAs are likely to deliver benefits to global species recovery and biodiversity. Considering the Global Biodiversity Framework's ambition of "30 by 30" (CBD, 2020), we highlight the importance for policy actions to include effective conservation management. Ultimately, protected areas across the globe can only provide real conservation benefits when they effectively buffer wild populations and habitats from human pressures on the environment (UNEP-WCMC and UNEP, 2021).

Code availability

All code was analysed in R using open-source packages and is available on request.

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CRediT authorship contribution statement

Caroline H. Brighton: Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Dario Massimino:** Formal analysis, Investigation, Supervision, Writing – review & editing. **Philipp Boersch-Supan:** Investigation, Methodology, Writing – review & editing. **Ailidh E. Barnes:** Methodology, Writing – review & editing. **Blaise Martay:** Methodology, Writing – review & editing. **Diana E. Bowler:** Investigation, Methodology, Writing – review & editing. **Hannah M.J. Hoskins:** Data curation, Writing – review & editing. **James W. Pearce-Higgins:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

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.

Data availability

The datasets generated and/or analysed during the current study are available in the Supplementary Information (in the Zenodo repository; https://doi.org/XXX). The raw BBS data are available upon request from the BTO, and the raw protected area condition data are available on request from the relevant statutory nature conservation body (Natural England, Natural Resources Wales, Northern Ireland Environment Agency and NatureScot).

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Appendix A. Supplementary data

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