Do conservation designations provide positive benefits for bird species and communities?

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There have been recent renewed commitments to increase the extent of protected areas to combat the growing biodiversity crisis, but yet the underpinning evidence for their effectiveness is mixed with causal connections rarely evaluated. We use data gathered by four large-scale citizen science programmes in the UK to provide the most comprehensive assessment to date of whether national (SSSI) and European (SPA/SAC) designated areas are associated with improved state (occurrence, abundance), change (rates of colonisation, persistence, and trend in abundance), community structure and, uniquely, demography (productivity) on a national avifauna, while controlling for differences in landcover, elevation and climate. Positive associations of with state suggest these areas are well-targeted, while positive associations with change tended to be restricted to rare and declining species and habitat specialists suggesting their benefit is greatest for the most conservation-dependent species. Associations with productivity suggest a plausible a demographic mechanism for positive effects of designation.

Introduction

The current high rate of biodiversity loss is one of the biggest global environmental issues, interacting with others to exceed environmental planetary boundaries (Rockstrom et al. 2009; Johnson et al. 2017). One approach to address this is to protect an increasing area of land and sea from anthropogenic threats (Schulze et al. 2018; Maxwell et al. 2020). Globally, the world has barely met the Convention of Biological Diversity Target 11 of at least 17% of terrestrial and inland water being designated for protection (UNEP-WCMC & IUCN 2021). Furthermore, there is a high degree of variation between countries (Buchanan et al. 2020), and effective implementation of the targets has been challenging overall (Xu et al. 2021). While protected areas (PA) vary in their aims there are, at root, three factors that determine their effectiveness: i) coverage, i.e. how much and what biodiversity is included within PA and how representative this is; ii) improved population status of focal species, i.e. are PA being managed well and external pressures minimised; and, more generally, iii) can they collectively facilitate the restoration or expansion of wider populations/habitats of conservation concern?

Given this diversity of outcomes, and wide variation in what protection means on the ground in terms of associated management practices, metrics to measure effectiveness can be difficult to construct (Rodrigues & Cazalis 2020) and evidence for the effectiveness of PA is mixed (Geldmann et al. 2019, Starnes et al. 2021). PA often target areas of greater species diversity, concentrations of species of conservation concern etc. (Kremen et al. 2008), but not always successfully (Venter et al. 2014; Cazalis et al. 2021). Regarding their impact, measures of PA extent can sometimes be positively associated with biodiversity trends, as measured by species' diversity (Cazalis et al. 2021) and population abundance trends (Gamero et al. 2017; Pellissier et al. 2020), although not always (Rada et al. 2019; Terraube et al. 2020, Duckworth & Altwegg 2018, Cunningham et al. 2021). Furthermore, as species' distribution changes lag behind those of climate (Lenoir et al. 2020), PA increasingly have a role in allowing populations to adapt to changing climates (Thomas & Gillingham 2015; van Teeffelen et al. 2015), although with high variability between species (Gillingham et al. 2015). Whether associations between PA and biological responses are a function of protection per se, or underlying patterns of land-use and habitat-type associated with their selection, is often unclear (Pellissier et al. 2020), and crucially, the variation in species' responses to PA remains largely unexplained. The causal links between PA and conservation outcomes are rarely tested (Geldman et al. 2013). We use a comprehensive assessment of the impacts of statutorily designated PA on the larger part of a national avifauna to address this lack of understanding around the underlying processes in order to better maximise the delivery of PA for biodiversity conservation.

Designating PA is a relatively straightforward policy tool to address biodiversity and there have been calls for an increased target of 30% coverage by 2030 (Waldron et al. 2020; Stokstad et al. 2021); implementing these effectively is, of course, a different matter. The large-scale, citizen-science based, biodiversity monitoring undertaken in much of Europe (Brlik et al 2021) provides an opportunity to quantify the wider benefits of designated area networks. Birds are amongst the best-studied taxa, with many species of high conservation concern and therefore the target of protection individually. In the UK, 29% of species are regarded as being of high conservation concern (Stanbury et al. 2021), with protection offered primarily by sites designated under either national (Sites of Special Scientific Interest, SSSI) or European (Natura 2000) legislation. SSSIs are given some protection against damaging operations and planned developments, whereas for Natura sites Member States are only obligated to take appropriate steps to avoid the effects of pollution or deterioration subject to an economic interest test; both largely fall into IUCN Protected Area Management Category IV, Dudley et al. 2008). As is increasingly common (Deguignet et al. 2017), these designations overlap and while SSSIs aim to protect representative habitats in a geographic area (not necessarily with a biodiversity focus), Special Protection Areas (SPA, under Directive EC/14/2009) and Special Areas of Conservation (SAC, EC/43/1992) are targeted at the “best” locations for, respectively, particular bird species and biodiversity/habitats more generally.

We use data gathered from four large-scale citizen-science programmes to test, whether, across the majority of the avifauna, PA are associated with (i) higher probabilities of occurrence and greater abundances, i.e. a better biodiversity ‘state’, and whether they are associated with positive changes in that, i.e. (ii) greater probabilities of persistence (equivalently, lower extinction risk) or colonisation and/or (iii) more positive (or less negative) trends in abundance. Further, we might expect (iv) that PA targeted at (particular) bird species (SPA) have a greater positive effect on bird populations generally than those designated for other biodiversity/environmental features (SAC). Importantly, in doing these comparisons we control for differences in landcover, elevation and climate to increase the likelihood of responses being directly a function of PA status. We also test (v) whether the variation in response between species is linked to changes in breeding success, a key potential mechanism. We then identify the species which PA most benefit, specifically testing (vi) whether PA benefit species that are rare, have declining population trends, or are habitat specialists (often those of most conservation concern, Hayhow et al. 2019). Finally, (vii) we consider whether the communities in areas with greater PA extent are more diverse, more specialist, or provide a refuge for cold-adapted species, testing their relevance for climate change adaptation.

Results

Are species more frequent or abundant in protected areas?

Many species occurred more frequently, and more abundantly, in areas with a greater extent of PA (Fig. 1). While there were a wide range of individual species’ responses, 47% of species had a significant positive association (compared to 20% negatively) between their likelihood of occurrence and extent of PA (no. species with significantly positive responses vs. no. species with significantly negative species: $\chi^2 = 18.7$; $P < 0.001$, Table S1), with a positive mean association between occurrence and PA extent (mean slope = 0.55 ± 0.10, Table S2). Similarly, the abundances of 47% of species were significantly positively associated with PA extent ($\chi^2 = 8.1$, P = 0.004), again with an overall positive mean association (0.25 ± 0.05). Thus, there was support for our first hypothesis, that species occur more often and more abundantly where there is a greater extent of PA.

Do protected areas promote positive change in status?

Although the absolute number of species showing significant positive (25%) and negative (27%) associations between colonisation and PA extent was similar ($\chi^2 = 0.04$, P=0.83, Fig.1), there was a significant positive overall response, with species more likely to colonise tetrads with a greater extent of PA (mean effect: 0.25 ± 0.09; Table S2), reflecting particularly strong positive effects for a number of rare/localised species (see below). Species were also significantly more likely to persist in sites with a greater extent of PA (0.33 ± 0.13; Table S2), with a tendency for more species to have significantly positive (29%) than negative (19%) effects (Table S1).

We found no evidence for a significant effect of PA on abundance trends (Fig. 1), with an equal number of species (21%) having significant positive and negative effects (Table S1) and an overall mean effect that did not differ from zero (Table S2). Thus, there was evidence that range dynamics (the balance of colonisation and extinction), but not changes in abundance, were more positive in PA.

Does effectiveness vary with designation purpose?

As predicted, these patterns of association were strongest with SPA designation, with a greater number of species being more likely to occur (42% significantly positive vs 27% significantly negative), or have higher abundances (40% vs 26%), with increasing SPA extent (Fig. 1). In contrast, similar numbers of species were more or less likely to occur with increasing SAC extent (Table S1). Furthermore, the mean relationships for occurrence, colonisation, persistence and abundance, but not abundance trend were stronger in SPAs than SACs (Table S2). These results are thus consistent with our fourth hypothesis, that the most effective PA for birds were those designated specifically for birds.

Are responses linked to higher reproductive success?

Overall, variation in reproductive success between sites, for the subset of species with productivity data, was negatively correlated with PA extent and this effect was least marked in relation to SPA extent (Table S2). On sites occurring in the vicinity of SPAs (but not SSSIs or SACs), those species that exhibited higher productivity with greater PA extent were also those that had higher abundances with more PA (Fig. 2a; Table S3). Furthermore, those species for which productivity tended to increase more over time in PA also tended to show more positive abundance trends with greater PA extent (Fig. 2b). Thus, comparison of two independent datasets provides support for our fourth hypothesis that higher productivity in PA is associated with more positive trends in abundance.

Which species benefit most from protected areas?

After accounting for body mass and phylogenetic relatedness, and weighting estimates to reduce the influence of species with uncertain responses, positive relationships between the extent of PA and occurrence, colonisations, persistence and abundance were most apparent for rare species (low population size) and habitat specialists (Fig. 3). Furthermore, species which were declining nationally had more positive (or less negative) trends in abundance in sites with greater PA extent (Fig. 4); relationships which were generally stronger with SPA than SAC extent (Table S4). Similarly, occurrence species that were legally protected or of conservation concern were higher, and significantly more so than for unlisted/green species, where there was greater PA (Table S5). However, the effect of PA extent on abundance of listed species was less marked, and when their, generally smaller, population size was accounted for, there were fewer significant differences between the species groupings, although the overall pattern of benefit remained (Table S6). Hypothesis (vi) was therefore supported with habitat specialists and rare (and declining) species most positively associated with PA.

Wetland and woodland species were more likely both to occur and persist in sites with a greater extent of PA, and occur in higher abundances, while species associated with urban environments were less likely to do so (Fig. 3, Table S4). Wetland, but not woodland, species also showed more positive abundance trends with greater PA extent, while urban species occurred at lower abundances (but also with more positive population trends).

Do protected areas change bird communities?

Overall species richness was generally lower where there was more PA, but the diversity of those species on SPA (only) was higher (Fig. 5). Sites with greater PA coverage supported more specialist and more cold-dwelling species, but also experienced reductions in species diversity over time and a shift towards more cold-dwelling communities. Thus hypothesis (vii) is partially supported in that communities in areas with greater PA cover are more specialist and cold-adapted, but only those with bird-focussed PA are more diverse.

Discussion

Through our comprehensive assessment, we highlight a range of associations that are consistent with the PA network having had a positive impact on bird conservation over the last three decades, in one of the least biodiverse nations with significant shortfalls in PA coverage (Starnes et al. 2021). Specifically, for rarer, declining or habitat specialist species, PA were associated with higher probabilities of occurrence and colonisation and lower rates of extinction. Furthermore specialists were more abundant and declining species had less negative trends in abundance, strongly suggesting that the benefits of this network are greatest for species most in need of conservation action. In the context of uncertain biodiversity responses to PA, and global ambitions to increase PA extent to address the current biodiversity crisis, these headlines add weight to the importance of countries living up to the ambitious target for 30% terrestrial and freshwater protected area coverage as an appropriate contribution to addressing the global biodiversity crisis (Waldron et al. 2020), but also emphasise the importance of appropriately targeting and managing them.

By controlling for large-scale variation in land-cover, topography and climate, we show that species were not only more likely to occur in PA, over and above the surrounding land characteristics (a much debated question; Cunningham et al. 2021), but extend that to show that PA are also effective in positively altering species dynamics, particularly of those species of most conservation interest (i.e. those with smaller or declining population sizes). Whilst it is difficult to completely separate the effects of protection and landcover, since, by definition, PA target particular habitats, for instance, wetland species were almost universally associated with PA since wetlands are a particularly threatened, and hence protected, habitat in the UK, we do provide evidence for an underlying mechanism of these positive effects on demography. Thus, those species with the most positive effects of PA on their status and trend also show higher rates of breeding success in PA. There is growing evidence in support of management interventions being effective in boosting the breeding success of birds of conservation concern (Franks et al. 2018, Pearce-Higgins et al. 2019), contributing to positive associations between those species and protected areas (Gillingham et al. 2015, Franks et al. 2018, Jellesmark et al. 2021), and the potential to stem or reverse species declines more generally (Morrison et al. 2021). The lack a positive relationship between productivity and PA extent and abundance trend across species (Table S3), suggests either that PA are not associated with greater habitat quality (and many are in 'unfavourable' condition, Starnes et al. 2021) or, given that they tend to be associated with greater rates of occurrence and higher abundance, there may be density-dependent limits to productivity in PA.

The effects were strongest for SPAs, that is areas specifically designated under European legislation for protecting birds, particularly rarer and declining habitat specialists. This supports the results of continent-wide associations (Donald et al. 2007), and previous single-species analyses (Franks et al. 2018, Jellesmark et al. 2021). Importantly, the effects we found were present despite wide variation in the intensity of site management of the PA (Starnes et al. 2021), which we did not account for. These effects may have been more pronounced were we able to account for the habitat quality of these sites, which may be as important as their size and quantity. Thus, positive effects of PA extent were most apparent for species associated with woodland and wetland habitats, both relatively rare and fragmented natural or semi-natural habitats in the British countryside (Martay et al. 2018) that have been the target of much conservation effort. The pattern of increased abundance of urban species is indicative of wider increases in generalist species (Sullivan et al. 2016) and outside pressures on PA generally. While the lack of a general relationship with abundance trend may indicate that PA are not being appropriately managed, the interpretation of such patterns is complex and requires detailed consideration (Wauchope et al. 2021).

We also show that responses at the species level scale-up to alter bird communities, with PA associated with reduced diversity and more negative diversity and evenness trends, potentially driven by complex responses across species as not all threatened habitats support high species richness or diversity (e.g. Sullivan et al 2016). Associations between PA extent and metrics of habitat (CSI) and thermal (CTI) specialisation show that areas with a greater PA extent support communities that tend to consist of more habitat specialists and cold-adapted species. Furthermore, rates of increase in CTI, a key signal of climate change impacts on bird communities (Devictor et al. 2012), are reduced in areas with a greater extent of PA suggesting PA have played a role in ameliorating these impacts. Similarly, analyses of breeding bird data from Finland show that declines in retreating northern species were less in PA than outside (Lehikoinen et al. 2019), and that in the UK, local extinctions of northern bird species at low elevations / latitudes were reduced by PA (Gillingham et al. 2015). Interactions between temperature-related community changes and either PA status (Gaüzère et al. 2016) or the extent of semi-natural habitat (Oliver et al. 2017; Neate-Clegg et al. 2018) provide further evidence that PA networks can modify community-level responses to climate change, particularly by facilitating climate-driven colonisation of new sites (Thomas et al. 2012, Hiley et al. 2013, Gillingham et al. 2015).

We provide arguably the most comprehensive assessment to date of the effects of protected sites on a national avifauna, documenting significant positive responses in species occurrence and abundance, particularly for rare and habitat specialists of conservation concern, that are impacting bird communities in those PA, and potentially increasing their resilience to impacts of climate change. While we have also provided unique evidence linking the potential benefit of PA to greater breeding success, further work is required to assess the extent to which the simple protection of rare habitats is sufficient. In the context of habitats that are otherwise being lost outside of PA this alone could account for a positive effect, but many of the species considered here (such as those that are rare and/or declining) are also subject to active management, especially on PA, further contributing to the positive responses. At a time of debate about the need to expand the coverage of global PA from the current level of around 17% to 30% by 2030, these findings provide strong evidence to support the contention that such a policy would be likely to deliver significant biodiversity benefit. The fact that responses were greatest for the SPA network (i.e. targeted at protecting bird habitats) suggests that in order to maximise their effectiveness of any new PA networks, new networks need to be targeted towards the species and habitats that are most threatened.

Methods

Data sources

Species occurrence, colonisation and persistence

We estimated species' breeding occurrence, colonisation and persistence from two nationwide Atlas surveys of the UK avifauna undertaken in 1988-91 (Gibbons et al. 1993) and 2007-11 (Balmer et al. 2013). Volunteer surveyors recorded the presence of each species in each of 42,561 and 46,390 2x2 km squares (tetrads) in the two Atlas periods; 29,851 of these tetrads (of a possible 61,843) were surveyed in both periods (Gillings et al. 2019). The tetrads covered the whole of the UK and with at least some coverage within each 10km square, except in Northern Ireland where tetrads were surveyed from within every second 10km square. Coverage was generally higher in areas with higher human population density (Fig. S1).

Species' occurrence, colonisations and persistence were assigned using presences and absences from the Atlas data. Species were classified as occurring in a tetrad if it was recorded in either survey period. Species were classified as colonising if they were absent in a square in the 1988–91 Atlas but present in the 2007–11 Atlas, thus only squares for which no presence of the species was recorded in the early Atlas were included in this analysis. Species were classified as persistent if they were present in both the 1988–91 and the 2007–11 Atlas, so only squares with the species in question present in the early Atlas were included in this analysis. Persistence is the complement of extinction rate (i.e. Persistence = 1 – Extinction) which we used to ensure positive estimates had a consistent interpretation across metrics.

Species sightings were designated as possible, probable or confirmed breeders. To exclude birds that may not have been breeding birds, we excluded sightings that had no probable or confirmed breeders of that species within their 10km square; 241 species met this criterion, but we excluded non-native species and species which occurred in fewer than 20 tetrads, leaving 180 species (Suppl File 1).

Species abundance and trend

Species abundance (and population trend) data were derived from the annual BTO/JNCC/RSPB Breeding Bird Survey (BBS) for the period 1994-2019 (Freeman et al. 2007). Briefly, volunteer surveyors record all adult birds they see or hear on two, 1km line-transects traversing a 1km square on two visits in the breeding season (early visit - 1st April-15th May and late visit - 16th May-30th June). Squares are selected according to a stratified random design that accounts for the number of volunteers available in each of 83 geographic regions, with a total of 6,718 squares covered (Fig. S1, increasing from 1,570 squares in 1994 to 4,005 surveyed in 2019). Our measure of square-level annual abundance was the maximum count of each species from the two visits to each square in a year. We considered 133 species (Suppl File 1) recorded in and average of at least 100 squares per year over the period (1994-2019) and, as above, excluded non-native species and records of likely non-breeding species (e.g. Fieldfare *Turdus pilaris*, flocks of waders). Seabirds, except gulls and terns, were also excluded due to poor coverage of their coastal breeding habitat in BBS squares. A small number of sites in upland areas (~100) included an adjacent square (so a 2km transect) to maximise the number of records in poorly covered areas with a low overall density of birds, which we accounted for with an offset in the models.

Productivity and productivity trend

We estimated productivity (number of young birds fledged per adult) from a constant effort mark-recapture program (CES, Robinson et al. 2009) for the years 1990 (when 97 sites operated) through to 2019 (114 sites), with a total of 490 sites (Fig. S1). Briefly, volunteers erect mist-nets in set positions for a set length of time on, usually, 12 visits through the breeding season. The total number of juveniles caught relative to the number of adults in each year provides an index of overall productivity for the site and immediately surrounding area. Capture totals for a site were omitted from the dataset if fewer than four early (from the first six) and four late (from the last six) visits were made at a site in any given year, to minimise the effect of any missing visits (Cave et al. 2009), or if fewer than 10 juveniles and adults of a species were caught in a year. A total of 22 species were included (Suppl. File 1).

Designated Areas and environmental data

Location and extent of designated areas (Fig. S2) were obtained from the Natural England Open Data Geoportal (https://naturalengland-defra.opendata.arcgis.com/), the Scottish spatial data portal (https://spatialdata.gov.scot/geonetwork/srv/eng/catalog.search), the Welsh Geo-portal (Lle, https://lle.gov.wales/catalogue) and OpenDataNI (https://www.opendatani.gov.uk/); all accessed on 1 November 2020. We extracted shapefiles for SSSIs, SPAs and SACs and calculated the proportion coverage within the land area of each 1km square (abundance, trend, productivity) or 2km square (occurrence, colonisations, persistence). Obtaining definitive designation dates (many of which will pre-date our dataset as about 50% of the UK network had been designated by 1974, Cunningham et al. (2021)) is difficult due to alterations in site boundaries over time and the lag between designation and management starting. Thus, we treat all sites as designated for the duration of our time period.

We extracted habitat data from the Land Cover Map 2015 (1km percentage aggregate class from Great Britain and Northern Ireland) (Rowland et al., 2017a, b). The aggregate land cover classes (and % cover) are Broad-leaved woodland (7.4); Coniferous woodland (4.9); Arable (24.7); Improved grassland (32.7); Semi-natural grassland (8.0); Mountain, heath and bog (10.4); Saltwater (0.7); Freshwater (1.2); Coastal (2.1); and Built-up areas and gardens (8.0). Mean elevation was calculated from the ASTER Global Digital Elevation Model v003 (NASA et al. 2019) for each 1km cell.

Species traits

Body mass is broadly correlated with many aspects of life history and was used as a proxy for these (Suppl. File 1). Mean body mass for all species was taken from Robinson (2005). Legal protection is afforded to species on Schedule 1 of the Wildlife and Countryside Act (1981, as amended) at a national scale and on Annex 1 of the Directive on the conservation of wild birds (EC/14/2009, the Birds Directive) at a European scale. Conservation status was taken from the first Birds of Conservation Concern list (Gibbons et al. 1996), which categorised species into three categories according to their, then, perceived vulnerability in relation to population size, range and abundance trend as: Green (least concern), Amber and Red (highest concern). Population size in the early 1990s and late 2010s was derived from the work of the Avian Population Estimates Panel (Stone et al. 1997; Woodward et al. 2020), and national population change taken as the ratio of these two numbers. The primary habitat each species occurred in was taken from Gibbons et al. (1993) and the degree of habitat specialization of each species using the species specialization index (SSI) of Sullivan et al. (2016).

Data Analysis

Overall approach

Firstly, for each species and population metric (occupancy, abundance etc.), we fitted a generalised additive model (GAM) (described below) to estimate the relationship between the population metric and the area of designated land within a (1km or 2km) survey square, whilst accounting for variation in habitat and climate. The coefficients from these individual species models for occurrence (and changes in this through colonisations and persistence), abundance (and linear trend in this over time), were then analysed using four general linear models (GLMs) for each population metric. The first three GLMs each had a single response variable of each type of conservation status traits (BoCC, Annex 1, Schedule 1), since we were interested in the importance of PA for these designated species. We then fit a fourth GLM to explore the role of underlying ecological traits in determining the strength of a species' response to the extent of designated area. In this last model, the species-specific effect estimates were weighted by the inverse of their variance to give greater weighting to those species that were estimated with more confidence. All analyses were carried out in R 4.0 (R Core Development Team, 2020).

In all these analyses we initially investigated how population metrics varied in relation to the area of designated land (of any type) within a survey square and then repeated the analyses three times, using the area of SSSI, SPA and SAC as the response variables (Fig. S2)

Species models

Measures of bird occurrence, colonisation, persistence, abundance, abundance trend and productivity for each bird species (where appropriate, see below) in each square, in each year were modelled using GAMs in the *mgcv* package (Wood 2017). We accounted for variation in climate by including a tensor smooth function of elevation, easting and northing; weather by including year (as a factor) as a random effect (in the abundance and productivity models); and habitat by including a linear functions of nine habitat types (we excluded the Arable category to avoid overfitting and parameter identifiability issues as the habitat coverages would otherwise sum to 1). For the abundance models we also included a quadratic function of year (continuous) to account for any overall long-term changes in the population size. Our focus was then on the linear term for the proportion of each survey square that was designated and, for the abundance and productivity analyses, the interaction of this term with (linear) year as a measure of the influence of PA extent on trends in these over time.

Species' occurrence, colonisations and persistence were all binary variables which we modelled with a binomial distribution and a logit link function. Models were assessed using the gam.check function in the DHARMa package (Hartig 2020) and species with over-dispersed and zero-inflated models were excluded. We also excluded a few species for which the parameter estimates were extreme outliers compared to parameter estimates for other species as this was likely to indicate poorly fitting models. The number of species for which the models were successful varied depending on the type of PA considered as an explanatory variable but occurrence, colonisation and persistence models could be run for 177 - 179 species (of the 180 for which we had data, see above), 164 - 165 species and 129 - 130 species respectively, depending on PA type.

Abundance (and trend therein) was modelled with negative binomial distribution (and a log link function) since Poisson models generally exhibited substantial overdispersion. Model fit was assessed using the gam.check function in the mgcv package (Wood 2017). We fitted models for all 133 species.

For productivity, the proportion of a year's CES captures that were juvenile was modelled as a binomial process with a logit link in an events-trials formulation (where each juvenile individual counted as a 'success', Robinson et al. 2009). We fitted these models for 22 species.

Summarising the responses

We summarised the correlation between species' population measures (i.e. occurrence, colonisation, persistence, abundance and trend) and the proportion of the square which was designated in two ways. Firstly, for each of the population measures, we compared the number of species with significantly positive associations with area of designation (and each type of designation separately) to the number of species with significantly negative associations using a one-sample binomial test. Secondly, for each of the population measures, we compared the mean across species of the associations with area of designation (and each type of designation separately) using t-tests. We then compared the response of species to SPAs and SACs by using paired t-tests to compare the association between species' population measures and SPA area with the same association with SAC area.

Traits analysis

To determine which traits were associated with a stronger positive response to PA extent, we fitted linear models with the extent of designated area coefficient (from the previous analysis for the individual species models) as the response variable and measures of conservation concern or ecological traits as explanatory variables. To account for phylogenetic relatedness between species we used an Ericson phylogenetic tree averaged from 1000 trees downloaded from birdtree.org (Jetz et al. 2012, accessed 8th March 2021) and performed a phylogenetically-weighted regression using the MCMCglmm (Hadfield 2010) and ape (Paradis et al. 2004) packages.

We fitted four models for each type of designation, each with different covariates: the three measures of conservation concern were analysed as three separate models and included log population size to account for the fact that commoner species tended to have more precise estimates and hence weighted more heavily in the analyses. A fourth model contained all the ecological traits (log body mass, log population size and change, species specialization index and habitat indicator status/association). We did not do a traits analysis on productivity since there were too few species.

Community analysis

We treated community metrics similarly to the species measures (described above) in the sense that we had one measure per BBS square per year derived from the species recorded in a given square and year. Before constructing the community indices we corrected the abundance measure by a species detectability factor (Johnston et al. 2014) to provide a more comparable measure of relative abundance across species. We considered three measures of community structure: species richness (number of species recorded), diversity (Hill's N_2, Hill 1973) and evenness (diversity divided by richness), and two synthetic trait measures the Community Specialisation Index (CSI, Julliard et al. 2006) and Community Temperature Index (CTI, Devictor et al. 2008). CSI is the density-weighted mean of the individual SSI for species occurring in a given square and measures the tendency for wildlife communities to increasingly consist of generalist species. SSI was calculated for each bird species as the coefficient of variation of the density of a species across 12 dominant habitat classes across all BBS squares (Sullivan et al. 2016). Similarly, CTI is the density-weighted average of individual Species Temperature Indices, the long-term average temperature over the species range, for which we use values derived from the full European breeding range (Devictor et al. 2012). For each of these metrics we fitted GAMs with appropriate distributions and landcover, climate variables along with the extent of designated area and its interaction with (linear) year.

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Contributions

J.W.P-H., D.G.N. and R.A.R conceived the study. A.B. undertook the analyses of BBS data and wrote the first draft, B.M. analysed the Atlas data and J.G.D. the CES data. S.J.H. organises the BBS and manages those data. All authors contributed critically to the final draft.

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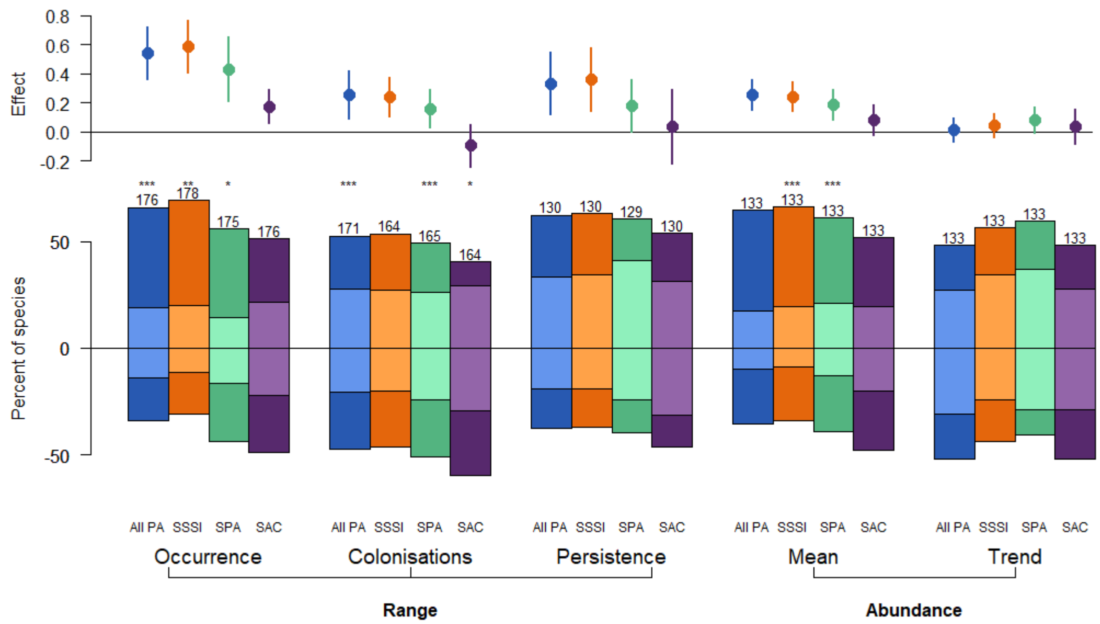

Figure 1 The bars (bottom) represent the percent of species and the points (top) represent the mean (and 95% confidence intervals) of effect sizes among individual species with negative and positive associations between the population measure (occurrence, colonisation, persistence, abundance and trend in abundance) and percentage cover of protected area within the monitored square. In the barchart, species with a significant relationship with the different designations are shown in dark colours while species with a non-significant relationship are shown in light colours. Numbers indicate the sample size for each and asterisks whether there is a significantly different proportion of species with significant positive effects compared to negative effects: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. The boxes in the upper panel indicate median, interquartile (box) and range (dotted lines) of the individual species effects.

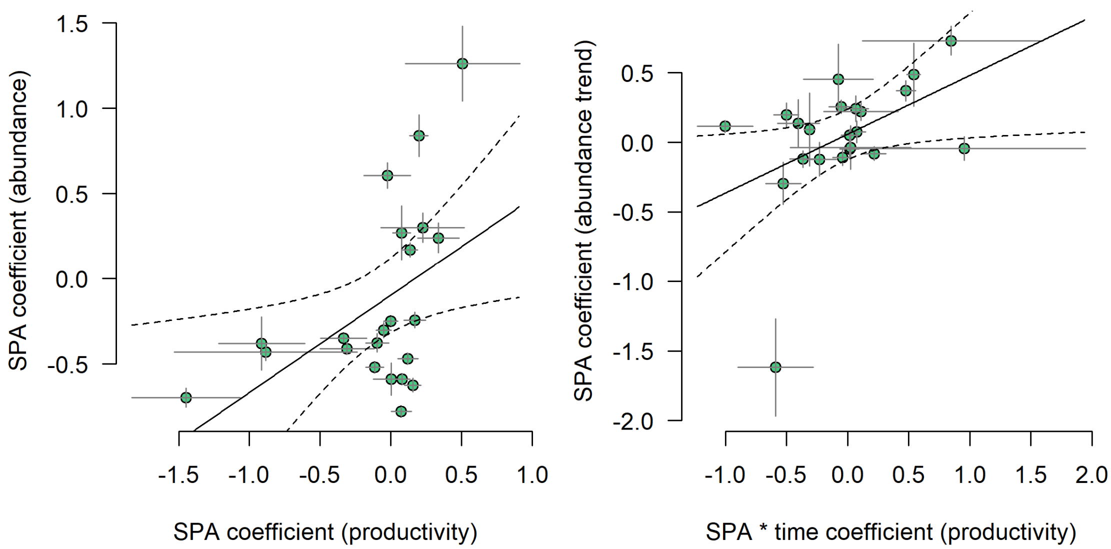

Figure 2 Relationship between productivity (CES) and abundance (BBS) PA coefficients (Table S3): a) productivity model SPA coefficients against abundance model SPA coefficients; b) productivity model SPA*time coefficients against abundance model SPA*time coefficients. The outlier in (b) is Cetti's warbler and excluding this point means the significance becomes marginal ($\beta = 0.23 \pm 0.11$, $p = 0.057$).

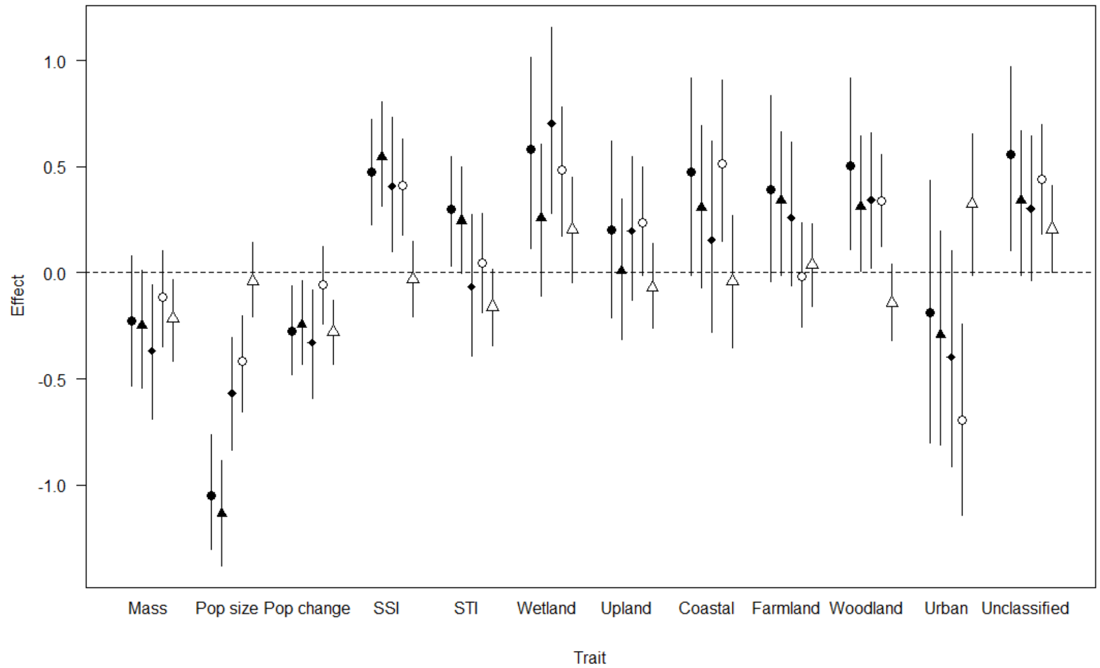

Figure 3 The extent to which the relationship between range (closed) and abundance (open) population measures and PA extent varies depending on species traits. The measures (± 95% confidence limits are, respectively, occurrence (closed circles), colonisation (closed triangles), persistence (closed diamonds), mean abundance (open circles) and abundance trend (open triangles). Mass, population size and population change are log-transformed values of mass, population size and population change. SSI and STI are the Species Specialisation and Temperature Indices. The final seven traits refer to the habitat in which species are most commonly found (Suppl File 1).

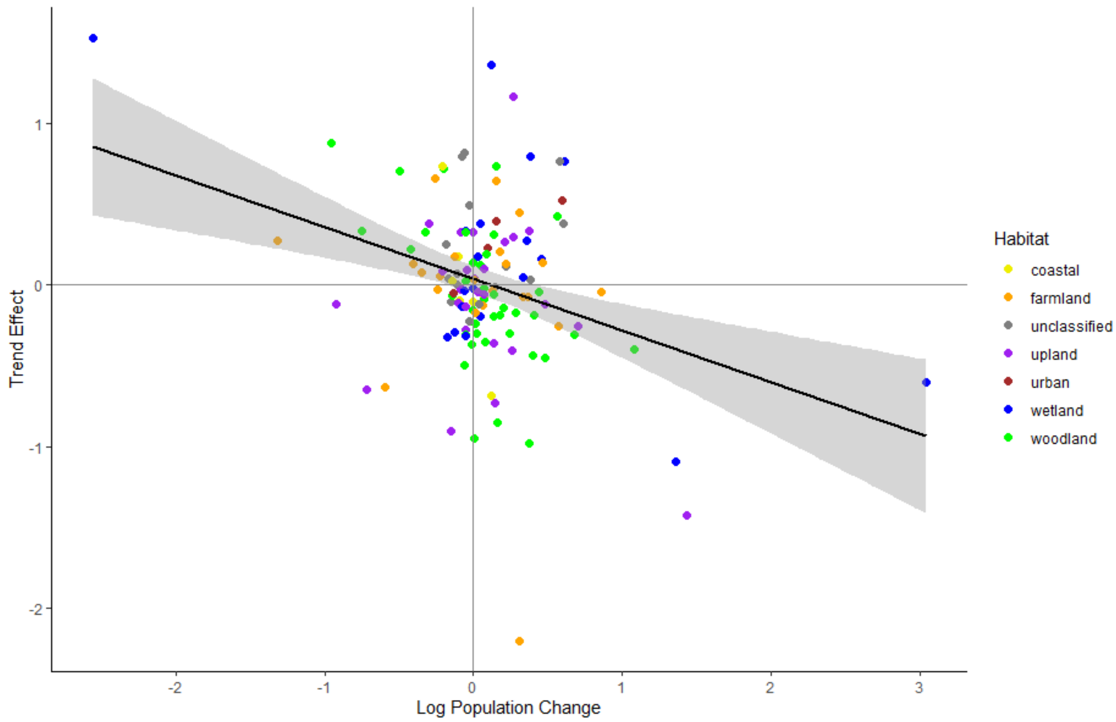

Figure 4 Declining species have more positive population trends where there is greater PA extent. Each point is a species estimate coloured by habitat preference, including the linear regression line (Table S4) and 95% confidence intervals (shaded grey).

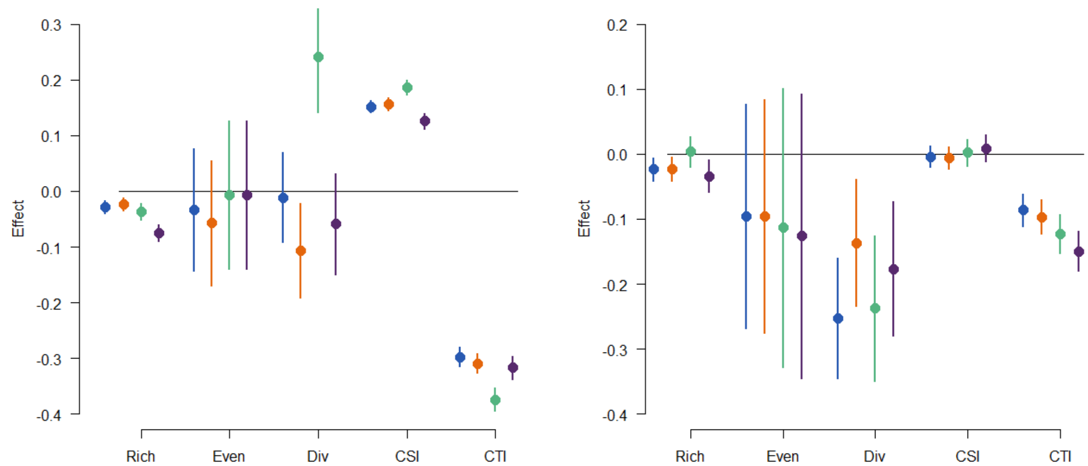

Figure 5 Effect of increased extent of protected area on metrics of community structure (species richness, evenness, diversity, Community Specialisation Index and Temperature Indices) (left) and trends in these (right). The relationship with all protected areas, SSSIs, SPAs and SACs are respectively shown in blue, orange, green and purple; bars represent 95% confidence limits of the estimates.

Table S1 Percentage of bird species influenced by extent of protected area, dividing species into those with significant and non-significant (in parentheses) positive and negative correlations between population measures and area of designation. The χ^2 values relate to a test of the difference in proportion of species with significantly positive or negative correlations with area of designation (* P<0.05, ** P<0.005, *** P<0.001).

	All Protected Areas					**SSSI**					**SPA**					**SAC**				
	+	**(+)**	**(-)**	**-**	**χ^2**	**+**	**(+)**	**(-)**	**-**	**χ^2**	**+**	**(+)**	**(-)**	**-**	**χ^2**	**+**	**(+)**	**(-)**	**-**	**χ^2**
Occurrence (n=179)	47.2	18.8	14.2	19.9	18.7***	48.9	20.2	11.2	19.7	21.3***	41.7	14.3	16.6	27.4	4.8*	29.5	21.6	22.2	26.7	0.2
Colonisation (n=165)	25.1	27.5	20.5	26.9	< 0.1	26.2	27.4	20.1	26.2	< 0.1	23.0	26.1	24.2	26.7	0.3	11	29.3	29.3	30.5	14.1**
Persistence (n=130)	29.2	33.1	19.2	18.5	2.7	28.5	34.6	19.2	17.7	2.8	19.4	41.1	24.0	15.5	0.4	22.3	31.5	31.5	14.6	1.7
Abundance (n=133)	47.4	17.3	9.8	25.6	8.1**	46.6	19.5	9.0	24.8	8.3**	39.8	21.1	12.8	26.3	17.5***	32.4	19.5	20.3	27.8	0.3
Abundance Trend (n=133)	21.1	27.1	30.8	21.1	< 0.1	21.8	34.6	24.1	19.5	0.1	22.6	36.8	28.6	12.0	3.7	20.3	27.8	28.6	23.3	0.2
Productivity (n=22)	13.6	18.2	27.3	40.9	2.1	13.6	18.2	31.8	36.4	1.5	22.7	31.8	31.8	13.6	0.1	13.6	18.1	22.7	45.5	2.8
Productivity Trend (n=22)	18.2	27.3	22.7	31.8	0.4	18.2	27.3	22.7	31.8	0.4	13.6	36.4	22.7	27.3	0.4	22.7	27.3	18.2	31.8	0.1

Table S2 Mean association between demographic characteristics of individual species and protected area extent within the survey square (± standard error), and (final column) the results of the t-test comparing the mean of SPA with SAC. Asterisks indicate significant differences from zero (* P<0.05, ** P<0.005, *** P<0.001).

	N Spp	All PA	SSSI	SPA	SAC	SPA vs SAC
Occurrence	179	0.549 ± 0.095***	0.585 ± 0.094***	0.430 ± 0.114***	0.174 ± 0.062***	t = 3.0**
Colonisations	165	0.252 ± 0.088**	0.237 ± 0.073**	0.157 ± 0.07*	-0.097 ± 0.077	t = 3.6***
Persistence	130	0.331 ± 0.128*	0.358 ± 0.133*	0.18 ± 0.109	0.032 ± 0.154	t = 2.1*
Abundance	133	0.252 ± 0.053***	0.24 ± 0.052***	0.19 ± 0.053***	0.08 ± 0.052	t = 2.3*
Abundance trend	133	0.012 ± 0.043	0.04 ± 0.043	0.08 ± 0.048	0.03 ± 0.061	t = 1.0
Productivity	22	-0.181 ± 0.080*	-0.183 ± 0.078*	-0.095 ± 0.097	-0.252 ±0.123	t = -1.1
Productivity trend	22	-0.067 ± 0.064	-0.065 ± 0.064	-0.035 ± 0.099	0.120 ± 0.167	t = 1.4

Table S3. Association between the relationship of demographic parameters to PA extent and that of productivity to PA extent for 22 species. The final row compares the association of PA and abundance trend with that of trend in productivity and PA extent. Slope coefficient parameters ± standard errors are shown, asterisks indicate significant differences from zero (* P<0.05, ** P<0.005, *** P<0.001).

Parameter	All PA	SSSI	SPA	SAC
Occupancy	0.024 ± 0.073	0.031 ± 0.074	0.046 ± 0.060	-0.143 ± 0.080
Colonisations	0.510 ± 0.442	0.470 ± 0.459	0.531 ± 0.274	-0.291 ± 0.204
Persistence	0.549 ± 0.453	0.564 ± 0.463	0.372 ± 0.283	-0.363 ± 0.274
Abundance	0.478 ± 0.415	0.468 ± 0.434	0.570 ± 0.247*	-0.430 ± 0.196*
Abundance Trend	-0.394 ± 0.181*	-0.349 ± 0.167*	-0.515 ± 0.197*	0.081 ± 0.137
Abundance Trend (vs Trend)	0.330 ± 0.242	0.331 ± 0.215	0.422 ± 0.203*	0.054 ± 0.101

Table S4 Model estimates of the relationship between extent of designated protected area and species population metrics. Estimates are quoted as mean and 95% CI's, significant relationships are in bold.

	All PA	SSSI	SPA	SAC
Occurrence				
Log Mass	-0.224 (-0.532, 0.079)	-0.188 (-0.487, 0.108)	-0.091 (-0.38, 0.239)	**-0.314 (-0.542, -0.069)**
Log Pop Size	**-1.05 (-1.304, -0.764)**	**-1.031 (-1.265, -0.731)**	**-0.973 (-1.249, -0.738)**	**-0.744 (-0.984, -0.512)**
Log Pop Change	**-0.274 (-0.478, -0.06)**	**-0.291 (-0.501, -0.073)**	**-0.221 (-0.419, -0.023)**	-0.093 (-0.276, 0.102)
SSI	**0.473 (0.228, 0.723)**	**0.569 (0.315, 0.812)**	**0.463 (0.223, 0.718)**	**0.337 (0.118, 0.564)**
STI	**0.298 (0.034, 0.547)**	**0.351 (0.088, 0.632)**	0.219 (-0.037, 0.454)	-0.082 (-0.317, 0.178)
Wetland	**0.581 (0.113, 1.014)**	**0.579 (0.125, 1.009)**	0.36 (-0.177, 0.879)	0.154 (-0.135, 0.455)
Upland	0.202 (-0.214, 0.621)	0.282 (-0.099, 0.646)	0.128 (-0.376, 0.616)	0.133 (-0.118, 0.395)
Coastal	0.473 (-0.013, 0.92)	**0.526 (0.053, 0.93)**	0.355 (-0.204, 0.885)	-0.036 (-0.337, 0.262)
Farmland	0.391 (-0.041, 0.834)	**0.472 (0.081, 0.839)**	0.324 (-0.21, 0.834)	0.229 (-0.013, 0.512)
Woodland	**0.503 (0.11, 0.919)**	**0.526 (0.164, 0.888)**	0.251 (-0.279, 0.762)	**0.293 (0.07, 0.533)**
Urban	-0.187 (-0.803, 0.435)	-0.204 (-0.828, 0.412)	-0.141 (-0.792, 0.5)	-0.283 (-0.768, 0.24)
Unclassified	**0.555 (0.105, 0.97)**	**0.603 (0.179, 0.994)**	0.302 (-0.246, 0.801)	0.254 (-0.018, 0.509)
Colonisations				
Log Mass	-0.251 (-0.541, 0.01)	-0.219 (-0.468, 0.025)	-0.099 (-0.364, 0.211)	**-0.275 (-0.45, -0.108)**
Log Pop Size	**-1.135 (-1.379, -0.885)**	**-1.077 (-1.329, -0.828)**	**-1.04 (-1.263, -0.765)**	**-0.798 (-0.995, -0.591)**
Log Pop Change	**-0.244 (-0.433, -0.035)**	**-0.268 (-0.48, -0.059)**	**-0.233 (-0.419, -0.038)**	-0.111 (-0.28, 0.08)
SSI	**0.543 (0.315, 0.806)**	**0.601 (0.336, 0.833)**	**0.537 (0.308, 0.765)**	**0.347 (0.167, 0.536)**
STI	0.245 (-0.003, 0.497)	0.2 (-0.055, 0.46)	0.166 (-0.073, 0.422)	-0.152 (-0.358, 0.032)
Wetland	0.258 (-0.11, 0.608)	0.292 (-0.052, 0.597)	0.12 (-0.343, 0.532)	-0.039 (-0.273, 0.179)
Upland	0.011 (-0.313, 0.349)	-0.006 (-0.27, 0.284)	-0.018 (-0.445, 0.337)	-0.121 (-0.298, 0.06)
Coastal	0.306 (-0.072, 0.693)	**0.411 (0.069, 0.738)**	0.285 (-0.204, 0.701)	-0.262 (-0.53, 0.016)
Farmland	0.34 (-0.011, 0.664)	**0.369 (0.094, 0.649)**	0.367 (-0.069, 0.763)	**0.223 (0.039, 0.42)**
Woodland	**0.312 (0.008, 0.646)**	**0.281 (0.025, 0.56)**	0.196 (-0.192, 0.618)	0.133 (-0.044, 0.312)
Urban	-0.295 (-0.813, 0.196)	-0.33 (-0.79, 0.153)	-0.166 (-0.671, 0.334)	-0.296 (-0.61, 0.035)
Unclassified	0.341 (-0.013, 0.668)	**0.381 (0.09, 0.664)**	0.229 (-0.209, 0.603)	0.079 (-0.098, 0.271)

Persistence				
Log Mass	**-0.368 (-0.688, -0.056)**	**-0.388 (-0.711, -0.089)**	**-0.282 (-0.606, 0.011)**	**-0.417 (-0.709, -0.127)**
Log Pop Size	**-0.567 (-0.837, -0.304)**	**-0.554 (-0.817, -0.299)**	**-0.383 (-0.63, -0.094)**	**-0.431 (-0.676, -0.181)**
Log Pop Change	**-0.329 (-0.592, -0.082)**	**-0.364 (-0.609, -0.109)**	**-0.257 (-0.508, -0.014)**	**-0.437 (-0.661, -0.186)**
SSI	**0.408 (0.099, 0.731)**	**0.43 (0.093, 0.742)**	**0.544 (0.191, 0.843)**	**0.343 (0.031, 0.644)**
STI	-0.066 (-0.394, 0.273)	-0.031 (-0.368, 0.312)	-0.016 (-0.339, 0.307)	-0.201 (-0.512, 0.13)
Wetland	**0.704 (0.278, 1.156)**	**0.724 (0.284, 1.164)**	**0.602 (0.171, 1.043)**	**0.471 (0.047, 0.867)**
Upland	0.197 (-0.131, 0.55)	0.265 (-0.048, 0.592)	0.117 (-0.199, 0.442)	0.257 (-0.017, 0.575)
Coastal	0.155 (-0.278, 0.621)	0.23 (-0.226, 0.693)	0.157 (-0.256, 0.596)	0.018 (-0.416, 0.493)
Farmland	0.259 (-0.062, 0.616)	0.235 (-0.094, 0.599)	**0.336 (0.006, 0.684)**	**0.292 (0.007, 0.594)**
Woodland	**0.344 (0.02, 0.661)**	**0.333 (0.036, 0.661)**	0.268 (-0.051, 0.602)	0.232 (-0.05, 0.535)
Urban	-0.397 (-0.915, 0.103)	-0.42 (-0.928, 0.096)	-0.421 (-0.951, 0.126)	-0.251 (-0.724, 0.236)
Unclassified	0.303 (-0.035, 0.645)	**0.342 (0.024, 0.692)**	**0.382 (0.04, 0.727)**	**0.367 (0.084, 0.674)**

Abundance				
Log Mass	-0.115 (-0.348, 0.105)	-0.156 (-0.368, 0.097)	-0.105 (-0.358, 0.116)	**-0.305 (-0.516, -0.075)**
Log Pop Size	**-0.417 (-0.656, -0.204)**	**-0.405 (-0.617, -0.182)**	**-0.395 (-0.627, -0.174)**	**-0.460 (-0.698, -0.245)**
Log Pop Change	-0.058 (-0.241, 0.126)	-0.049 (-0.242, 0.114)	0.010 (-0.206, 0.184)	0.041 (-0.159, 0.232)
SSI	**0.412 (0.180, 0.631)**	**0.420 (0.184, 0.618)**	**0.468 (0.244, 0.707)**	**0.315 (0.076, 0.529)**
STI	0.047 (-0.186, 0.279)	0.029 (-0.207, 0.241)	-0.093 (-0.329, 0.133)	-0.007 (-0.245, 0.210)
Wetland	**0.483 (0.173, 0.781)**	**0.437 (0.117, 0.731)**	**0.303 (0.005, 0.604)**	-0.057 (-0.357, 0.249)
Upland	0.234 (-0.013, 0.499)	0.242 (-0.008, 0.494)	0.151 (-0.085, 0.405)	0.215 (-0.026, 0.442)
Coastal	**0.513 (0.150, 0.907)**	0.288 (-0.115, 0.675)	0.244 (-0.151, 0.636)	0.313 (-0.052, 0.702)
Farmland	-0.015 (-0.256, 0.237)	0.038 (-0.191, 0.284)	0.120 (-0.125, 0.361)	0.059 (-0.184, 0.303)
Woodland	**0.336 (0.126, 0.558)**	**0.342 (0.128, 0.567)**	**0.227 (0.015, 0.465)**	0.105 (-0.107, 0.318)
Urban	**-0.693 (-1.140, -0.243)**	**-0.670 (-1.122, -0.210)**	-0.318 (-0.765, 0.137)	**-0.778 (-1.205, -0.349)**
Unclassified	**0.441 (0.183, 0.699)**	**0.442 (0.177, 0.692)**	**0.387 (0.133, 0.659)**	**0.370 (0.112, 0.611)**

Trend				
Log Mass	**-0.217 (-0.414, -0.033)**	-0.182 (-0.380, 0.012)	-0.164 (-0.395, 0.058)	**-0.428 (-0.741, -0.155)**
Log Pop Size	-0.038 (-0.205, 0.144)	-0.029 (-0.205, 0.167)	-0.024 (-0.254, 0.176)	-0.121 (-0.384, 0.135)
Log Pop Change	**-0.279 (-0.431, -0.127)**	**-0.272 (-0.435, -0.115)**	**-0.315 (-0.491, -0.147)**	-0.186 (-0.415, 0.053)
SSI	-0.032 (-0.207, 0.148)	0.004 (-0.203, 0.176)	0.012 (-0.188, 0.218)	-0.037 (-0.287, 0.216)
STI	-0.159 (-0.344, 0.019)	-0.137 (-0.331, 0.061)	-0.027 (-0.264, 0.188)	**-0.338 (-0.618, -0.051)**
Wetland	0.202 (-0.046, 0.448)	**0.263 (0.013, 0.542)**	**0.330 (0.038, 0.623)**	**0.460 (0.078, 0.883)**

Upland	-0.071 (-0.262, 0.138)	-0.058 (-0.266, 0.167)	0.049 (-0.197, 0.293)	-0.133 (-0.445, 0.215)
Coastal	-0.041 (-0.351, 0.270)	0.120 (-0.215, 0.466)	0.141 (-0.229, 0.519)	-0.020 (-0.508, 0.501)
Farmland	0.036 (-0.158, 0.233)	0.031 (-0.178, 0.246)	0.003 (-0.222, 0.241)	0.057 (-0.280, 0.381)
Woodland	-0.143 (-0.318, 0.039)	-0.109 (-0.302, 0.098)	-0.010 (-0.212, 0.218)	-0.153 (-0.452, 0.159)
Urban	0.327 (-0.011, 0.654)	0.293 (-0.062, 0.642)	**0.404 (0.005, 0.814)**	**0.703 (0.184, 1.194)**
Unclassified	**0.206 (0.004, 0.411)**	**0.240 (0.018, 0.467)**	0.224 (-0.014, 0.478)	0.151 (-0.182, 0.505)

Table S5 Mean effect of extent of protected areas on population metrics of species of conservation concern (BoCC) or which are legally protected (Annex/Schedule 1). Asterisks indicate the significance of the difference in response to PA between species of conservation concern (red/amber-listed) and those not (green-listed) or for those designated under Annex 1 ('Birds' Directive) and Schedule 1 (UK Wildlife & Countryside Act) and those not so designated (. p < 0.1; * p < 0.05; ** p < 0.01; *** p < 0.001).

	All PA	**SSSI**	**SPA**	**SAC**
Occurrence				
BoCC Green	-0.075 (-0.175, 0.025)	-0.059 (-0.166, 0.048)	-0.237 (-0.339, -0.135)	-0.129 (-0.219, -0.039)
BoCC Amber	0.235 (0.088, 0.383)***	0.286 (0.128, 0.444)***	0.21 (0.063, 0.356)***	0.086 (-0.044, 0.217)*
BoCC Red	0.073 (-0.169, 0.314)	0.15 (-0.106, 0.406)	-0.019 (-0.264, 0.227)	0.02 (-0.197, 0.238)
Not Annex 1	0.002 (-0.079, 0.082)	0.031 (-0.055, 0.118)	-0.124 (-0.207, -0.041)	-0.078 (-0.149, -0.007)
Annex 1	0.535 (0.178, 0.891)**	0.62 (0.238, 1.003)**	0.606 (0.264, 0.948)***	0.419 (0.119, 0.719)**
Not Schedule 1	0.006 (-0.074, 0.087)	0.036 (-0.05, 0.123)	-0.112 (-0.196, -0.028)	-0.071 (-0.142, 0)
Schedule 1	0.586 (0.173, 0.998)*	0.673 (0.234, 1.113)*	0.597 (0.192, 1.002)***	0.451 (0.094, 0.808)*
Colonisation				
BoCC Green	-0.337 (-0.443, -0.231)	-0.327 (-0.438, -0.216)	-0.39 (-0.499, -0.28)	-0.34 (-0.426, -0.254)
BoCC Amber	0.064 (-0.094, 0.222)***	0.103 (-0.063, 0.269)***	0.093 (-0.064, 0.251)***	-0.084 (-0.211, 0.043)**
BoCC Red	-0.114 (-0.382, 0.154)	-0.051 (-0.331, 0.229)	-0.126 (-0.399, 0.148)	-0.169 (-0.387, 0.048)

Not Annex 1	-0.237 (-0.323, -0.151)	-0.215 (-0.306, -0.124)	-0.266 (-0.355, -0.177)	-0.274 (-0.343, -0.204)
Annex 1	0.547 (0.143, 0.95)***	0.578 (0.151, 1.004)***	0.603 (0.218, 0.988)***	0.233 (-0.084, 0.551)**
Not Schedule 1	-0.236 (-0.322, -0.15)	-0.212 (-0.303, -0.122)	-0.258 (-0.348, -0.168)	-0.271 (-0.34, -0.201)
Schedule 1	0.608 (0.185, 1.03)***	0.621 (0.168, 1.073)***	0.552 (0.136, 0.968)***	0.25 (-0.096, 0.595)**
Persistence				
BoCC Green	-0.061 (-0.198, 0.075)	-0.043 (-0.184, 0.098)	-0.069 (-0.201, 0.063)	-0.058 (-0.18, 0.063)
BoCC Amber	0.038 (-0.176, 0.251)	0.077 (-0.144, 0.297)	0.226 (0.029, 0.423)*	0.143 (-0.044, 0.33)
BoCC Red	0.064 (-0.269, 0.397)	0.106 (-0.236, 0.448)	-0.023 (-0.338, 0.292)	0.171 (-0.129, 0.471)
Not Annex 1	-0.036 (-0.144, 0.073)	-0.009 (-0.121, 0.103)	-0.001 (-0.106, 0.104)	0.002 (-0.095, 0.099)
Annex 1	0.634 (-0.125, 1.392)	0.661 (-0.137, 1.46)	0.727 (0.079, 1.375)*	0.689 (0.083, 1.296)*
Not Schedule 1	-0.026 (-0.134, 0.083)	0.001 (-0.111, 0.114)	0.016 (-0.09, 0.122)	0.017 (-0.081, 0.114)
Schedule 1	0.529 (-0.845, 1.903)	0.527 (-0.932, 1.986)	0.267 (-0.987, 1.52)	0.342 (-0.872, 1.555)
Abundance				
BoCC Green	-0.138 (-0.236, -0.041)	-0.126 (-0.222, -0.029)	-0.208 (-0.302, -0.114)	-0.184 (-0.271, -0.097)
BoCC Amber	-0.232 (-0.406, -0.057)	-0.230 (-0.405, -0.055)	-0.144 (-0.309, 0.021)	-0.195 (-0.349, -0.042)

BoCC Red	-0.048 (-0.326, 0.231)	-0.036 (-0.312, 0.241)	-0.033 (-0.292, 0.227)	-0.011 (-0.251, 0.228)
Not Annex 1	-0.159 (-0.240, -0.078)	-0.148 (-0.229, -0.068)	-0.19 (-0.267, -0.113)	-0.183 (-0.254, -0.111)
Annex 1	0.556 (-0.191, 1.303)	0.550 (-0.201, 1.300)	0.558 (-0.046, 1.162)*	0.553 (-0.004, 1.110)*
Not Schedule 1	-0.157 (-0.238, -0.076)	-0.146 (-0.227, -0.065)	-0.187 (-0.264, -0.109)	-0.179 (-0.251, -0.107)
Schedule 1	0.464 (-0.360, 1.287)	0.453 (-0.372, 1.278)	0.480 (-0.197, 1.157)	0.505 (-0.136, 1.146)*
Trend				
BoCC Green	-0.030 (-0.081, 0.022)	-0.017 (-0.069, 0.035)	0.046 (-0.013, 0.105)	-0.054 (-0.126, 0.017)
BoCC Amber	0.007 (-0.084, 0.098)	0.032 (-0.061, 0.124)	0.071 (-0.031, 0.172)	0.002 (-0.121, 0.125)
BoCC Red	0.106 (-0.037, 0.248)	0.086 (-0.058, 0.230)	0.102 (-0.056, 0.260)	0.105 (-0.085, 0.296)
Not Annex 1	-0.007 (-0.051, 0.036)	0.004 (-0.039, 0.048)	0.057 (0.008, 0.106)	-0.025 (-0.084, 0.035)
Annex 1	-0.135 (-0.501, 0.231)	-0.084 (-0.457, 0.289)	0.058 (-0.295, 0.411)	-0.116 (-0.543, 0.311)
Not Schedule 1	-0.006 (-0.049, 0.037)	0.007 (-0.036, 0.050)	0.061 (0.013, 0.110)	-0.022 (-0.081, 0.037)
Schedule 1	-0.317 (-0.715, 0.080)	-0.326 (-0.725, 0.072)	-0.197 (-0.583, 0.190)	-0.332 (-0.815, 0.150)

Table S6 Mean effect of extent of protected areas on population metrics of species of conservation concern (BoCC) or which are legally protected (Annex/Schedule 1), adjusted for the mean population size of species within the group. Asterisks indicate the significance of the difference in response to PA between species of conservation concern (red/amber-listed) and those not (green-listed) or for those designated under Annex 1 ('Birds' Directive) and Schedule 1 (UK Wildlife & Countryside Act) and those not so designated, after taking differences in population size into account (* p < 0.05; ** p < 0.01; *** p < 0.001).

	All PA	SSSI	SPA	SAC
Occurrence				
BoCC Green	-0.24 (-0.332, -0.149)	-0.231 (-0.329, -0.133)	-0.409 (-0.501, -0.317)	-0.252 (-0.339, -0.165)
BoCC Amber	0.462 (0.328, 0.597)	0.52 (0.377, 0.663)*	0.437 (0.307, 0.567)***	0.254 (0.129, 0.379)
BoCC Red	0.719 (0.468, 0.97)	0.845 (0.579, 1.111)	0.626 (0.38, 0.872)	0.515 (0.276, 0.754)
Not Annex 1	-1.448 (-1.787, -1.109)	-1.565 (-1.935, -1.195)	-1.603 (-1.944, -1.263)	-1.109 (-1.426, -0.792)
Annex 1	1.968 (1.523, 2.412)	2.19 (1.71, 2.67)	2.065 (1.629, 2.5)	1.455 (1.042, 1.867)
Not Schedule 1	-2.073 (-2.546, -1.6)	-2.228 (-2.739, -1.717)	-2.308 (-2.786, -1.829)	-1.564 (-2.008, -1.121)
Schedule 1	2.475 (1.927, 3.023)	2.73 (2.142, 3.319)	2.584 (2.041, 3.127)	1.819 (1.306, 2.333)
Colonisation				
BoCC Green	-0.56 (-0.654, -0.466)	-0.572 (-0.673, -0.471)	-0.615 (-0.714, -0.517)	-0.487 (-0.572, -0.401)
BoCC Amber	0.376 (0.238, 0.514)**	0.402 (0.257, 0.548)**	0.373 (0.235, 0.512)***	0.105 (-0.018, 0.228)*

BoCC Red	0.572 (0.323, 0.821)	0.588 (0.33, 0.845)*	0.442 (0.195, 0.69)	0.230 (0.011, 0.45)
Not Annex 1	-2.066 (-2.44, -1.692)	-2.015 (-2.403, -1.628)	-1.940 (-2.314, -1.567)	-1.37 (-1.691, -1.048)
Annex 1	2.245 (1.775, 2.716)	2.184 (1.699, 2.668)	2.095 (1.641, 2.55)	1.234 (0.832, 1.636)
Not Schedule 1	-2.645 (-3.137, -2.154)	-2.544 (-3.04, -2.048)	-2.492 (-2.97, -2.015)	-1.705 (-2.117, -1.292)
Schedule 1	2.754 (2.203, 3.305)	2.623 (2.065, 3.181)	2.469 (1.942, 2.996)	1.495 (1.028, 1.962)
Persistence				
BoCC Green	-0.09 (-0.217, 0.037)	-0.114 (-0.236, 0.008)	-0.087 (-0.199, 0.026)	-0.09 (-0.217, 0.037)
BoCC Amber	0.578 (0.319, 0.837)	0.604 (0.371, 0.838)	0.492 (0.269, 0.715)	0.578 (0.319, 0.837)
BoCC Red	0.348 (0.032, 0.663)	0.176 (-0.123, 0.475)	0.355 (0.068, 0.642)*	0.348 (0.032, 0.663)
Not Annex 1	-0.792 (-1.092, -0.493)	-0.682 (-0.966, -0.398)	-0.554 (-0.817, -0.291)	-0.792 (-1.092, -0.493)
Annex 1	1.367 (0.602, 2.133)	1.339 (0.698, 1.98)	1.202 (0.591, 1.813)	1.367 (0.602, 2.133)
Not Schedule 1	-1.164 (-1.578, -0.75)	-1.043 (-1.433, -0.654)	-0.855 (-1.219, -0.491)	-1.164 (-1.578, -0.75)
Schedule 1	1.291 (-0.043, 2.624)	0.95 (-0.206, 2.107)	0.913 (-0.23, 2.056)	1.291 (-0.043, 2.624)
Abundance				
BoCC Green	-0.172 (-0.253, -0.091)	-0.158 (-0.239, -0.076)	-0.237 (-0.316, -0.158)	-0.213 (-0.287, -0.139)

BoCC Amber	0.195 (0.016, 0.373)*	0.181 (0.000, 0.362)*	0.214 (0.048, 0.380)	0.130 (-0.026, 0.285)
BoCC Red	0.577 (0.300, 0.855)	0.568 (0.288, 0.847)	0.523 (0.263, 0.784)	0.500 (0.256, 0.744)
Not Annex 1	-1.305 (-1.627, -0.984)	-1.251 (-1.577, -0.926)	-1.25 (-1.553, -0.948)	-1.106 (-1.392, -0.819)
Annex 1	1.643 (0.941, 2.345)	1.594 (0.881, 2.308)	1.583 (0.993, 2.173)	1.455 (0.898, 2.013)
Not Schedule 1	-1.543 (-1.921, -1.166)	-1.482 (-1.864, -1.100)	-1.483 (-1.839, -1.126)	-1.307 (-1.645, -0.970)
Schedule 1	1.679 (0.911, 2.447)	1.622 (0.843, 2.402)	1.617 (0.966, 2.267)	1.487 (0.861, 2.113)
Trend				
BoCC Green	-0.028 (-0.080, 0.024)	-0.016 (-0.069, 0.037)	0.047 (-0.013, 0.106)	-0.053 (-0.125, 0.020)
BoCC Amber	-0.009 (-0.120, 0.101)	0.024 (-0.088, 0.137)	0.068 (-0.052, 0.188)	-0.015 (-0.160, 0.131)
BoCC Red	0.081 (-0.091, 0.253) (.)	0.075 (-0.100, 0.249)	0.098 (-0.092, 0.288)	0.078 (-0.151, 0.308)
Not Annex 1	0.008 (-0.193, 0.208)	-0.006 (-0.209, 0.196)	0.054 (-0.169, 0.276)	-0.014 (-0.287, 0.259)
Annex 1	-0.15 (-0.561, 0.261)	-0.075 (-0.493 0.343)	0.061 (-0.350, 0.472)	-0.127 (-0.626, 0.373)
Not Schedule 1	-0.026 (-0.260, 0.208)	-0.058 (-0.294, 0.178)	-0.013 (-0.274, 0.247)	-0.064 (-0.384, 0.255)
Schedule 1	-0.3 (-0.745, 0.146)	-0.27 (-0.717, 0.177) (.)	-0.132 (-0.578, 0.314)	-0.295 (-0.851, 0.260)

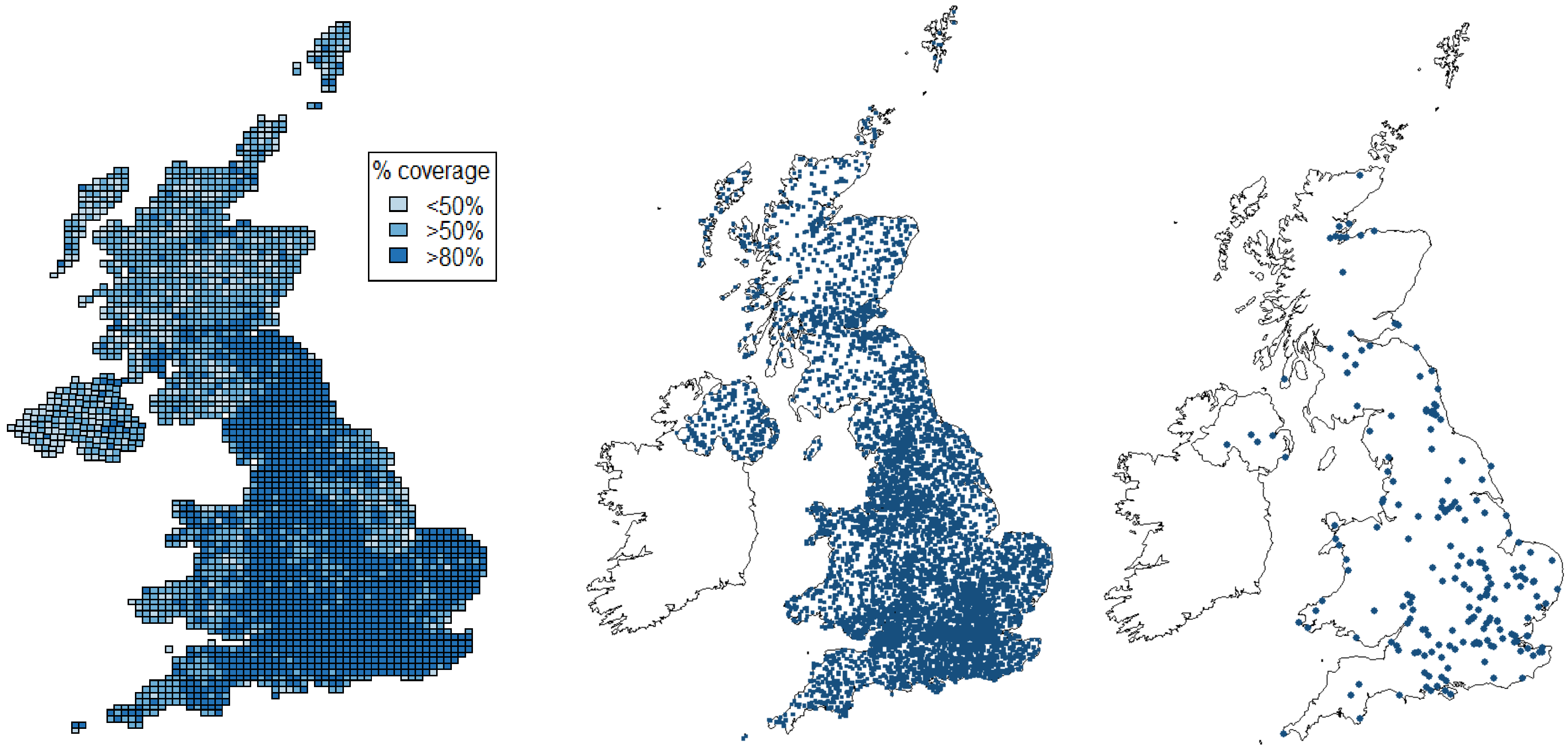

Figure S1. Percent of available 2km tetrads within each 10km square surveyed in either Atlas period (1988-91 or 2007-11, left), BBS survey squares (middle) and CES sites (right) contributing to the data.

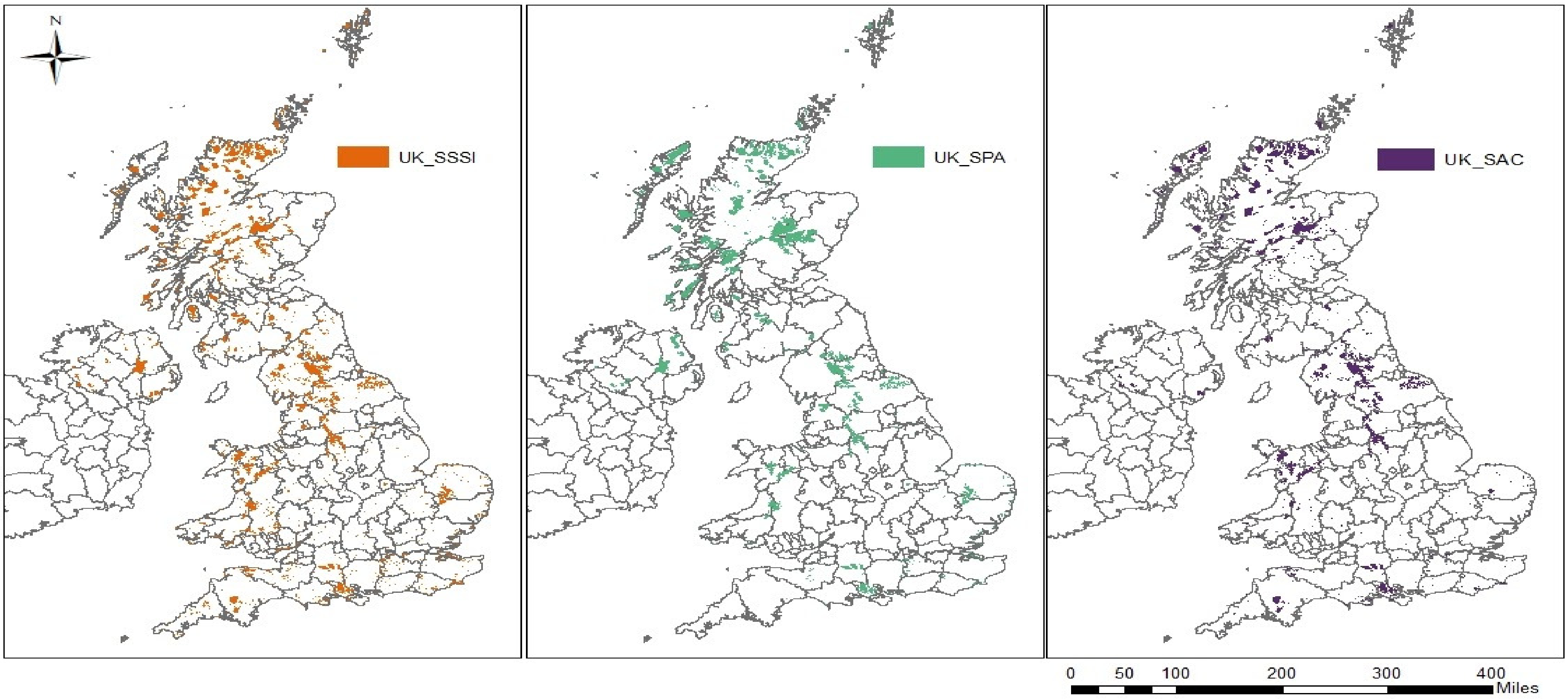

Figure S2 Maps of the three types of designated area in the UK