



Protected areas support more species than unprotected areas in Great Britain, but lose them equally rapidly

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ABSTRACT

Protected areas are a key conservation tool, yet their effectiveness at maintaining biodiversity through time is rarely quantified. Here, we assess protected area effectiveness across sampled portions of Great Britain (primarily England) using regionalized (protected vs unprotected areas) Bayesian occupancy-detection models for 1238 invertebrate species at 1 km resolution, based on ~1 million occurrence records between 1990 and 2018. We quantified species richness, species trends, and compositional change (temporal beta diversity; decomposed into losses and gains). We report results overall, for two functional groups (pollinators and predators), and for rare and common species. Whilst we found that protected areas have 15 % more species on average than unprotected ones, declines in occupancy are of similar magnitude and species composition has changed 27 % across protected and unprotected areas, with losses dominating gains. Pollinators have suffered particularly severe declines. Still, protected areas are colonized by more locally-novel pollinator species than unprotected areas, suggesting that they might act as ‘landing pads’ for range-shifting pollinators. We find almost double the number of rare species in protected areas (although rare species trends are similar in protected and unprotected areas); whereas we uncover disproportionately steep declines for common species within protected areas. Our results highlight strong invertebrate reorganization and loss across both protected and unprotected areas. We therefore call for more effective protected areas, in combination with wider action, to bend the curve of biodiversity loss – where we provide a toolkit to quantify effectiveness. We must grasp the opportunity to *effectively* conserve biodiversity through time.

1. Introduction

A major response to biodiversity loss has been the establishment of protected areas (Jenkins and Joppa, 2009), which have long been regarded as a cornerstone of the conservation movement (Craigie et al., 2010; Mace, 2014; Watson et al., 2014). However, to fulfil their role, protected areas need to be effective at conserving biodiversity. Protected area effectiveness depends on both the quantity (e.g., coverage) and quality (e.g., representativeness, good condition, high species richness, maintaining or increasing species' population sizes). The majority of global targets and progress assessments have focused on quantity, i.e., coverage (Rodrigues and Cazalis, 2020; Venter et al., 2014; Watson et al., 2014). For example, Aichi Target 11 aimed for the protection of 17 % of global terrestrial area by 2020 (but was not met) (UNEP-WCMC et al., 2020). An even more ambitious 30 % target by 2030 is anticipated

under the post-2020 Global Biodiversity Framework (Convention on Biological Diversity, 2020), and many governments have already committed to this ‘30 by 30’ goal (e.g., UK Government, 2020). While quantity is important, there are many examples of poor quality protected areas (i.e., paper parks; Coad et al., 2019; Craigie et al., 2010; Rodrigues and Cazalis, 2020), hence we require both quantity and quality for the delivery of effective protected areas. Drawing an analogy, it would be insufficient to monitor healthcare effectiveness based solely on available beds (i.e., quantity) irrespective of whether the health of patients is restored/preserved (i.e., quality) (Barnes et al., 2018; Edgar, 2017).

Protected area effectiveness, especially quality, has many different facets (Durán et al., 2022), reflecting the diverse objectives of protected areas. Much of the focus has been on the ability of protected areas to prevent or mitigate threats (Andam et al., 2008; Geldmann et al., 2019;

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Laurance et al., 2012), as well as on their management effectiveness (Coad et al., 2019; Geldmann et al., 2015; Gill et al., 2017; Leverington et al., 2010; Watson et al., 2014). However, the relationship of these measures to biodiversity is indirect and poorly understood (Craigie et al., 2010; Redford, 1992). By contrast, more direct measures of protected area effectiveness generally focus on 1) the state of biodiversity, such as representativeness (e.g., species representation) (Cunningham et al., 2021; Rodrigues et al., 2004) or levels of biodiversity relative to unprotected areas (e.g., greater species richness) (Gray et al., 2016); or 2) the maintenance of biodiversity through time, including species trends (Pellissier et al., 2020; Wauchope et al., 2022) or compositional change (Hiley et al., 2016). Still, empirical quantification of multiple facets of effectiveness within terrestrial protected areas is scarce and challenging to obtain (Bailey et al., 2022; Maxwell et al., 2020; Rodrigues and Cazalis, 2020).

Multi-faceted assessments of protected area effectiveness are especially scarce for terrestrial invertebrates, even though there is increasing evidence of invertebrate biodiversity declines and turnover (Powney et al., 2019; van Klink et al., 2020; Wagner, 2020). Hallmann et al. (2017) reported a > 75 % decline over 27 years in total flying insect biomass in protected areas across Germany. The magnitude of this effect is alarming, yet without a comparison to unprotected areas the context of this decline is difficult to assess. In addition, there is a growing appreciation of the ecological and economic importance of invertebrates (Losey and Vaughan, 2006; Schowalter et al., 2018). Invertebrates underpin multiple ecosystem functions, including pollination, biological control, nutrient cycling, and as a food source for higher trophic levels (Schowalter et al., 2018; Wagner, 2020). For example, an estimated 80 % of wild plants are dependent on insect pollination (Ollerton et al., 2011), while 50 % of bird species primarily rely on invertebrate prey (Cooke et al., 2020; Wilman et al., 2014). Indeed, greater invertebrate biodiversity within a functional group (e.g., pollinators) has the potential to insure ecosystem function flows against environmental perturbations, promoting resilient ecosystem function provision (Oliver et al., 2015; Yachi and Loreau, 1999). Protected areas therefore have an opportunity to support greater biodiversity and thus resilient ecosystem functions compared to unprotected areas (Bailey et al., 2022), with benefits for the wider landscape.

Here, we assess the effectiveness of protected areas across Great Britain at conserving multiple facets of terrestrial invertebrate biodiversity during the past three decades. Great Britain is a useful case study for investigating the effectiveness of protected areas (Cunningham et al., 2021), as it has one of the globe's most comprehensive biological records systems, including long-term invertebrate monitoring schemes (Pocock et al., 2015). This ensures that the status of invertebrates in Great Britain is relatively well-understood (Outhwaite et al., 2020) compared with the rest of the world (Cardoso et al., 2011). Great Britain is a nature-depleted region (e.g., 41 % of monitored species in the UK have declined since 1970 compared to 26 % that have increased; Hayhow et al., 2019), with fragments of semi-natural habitat across a landscape of human use and management (Lawton, 2010; Shwartz et al., 2017). However, similar situations occur across much of Europe (Critchlow et al., 2022), and increasingly in other regions. Our case study therefore provides an essential test of how effective protected areas are at conserving biodiversity, with a focus on both the state of biodiversity (species richness) and its maintenance through time (species trends, species composition) across a human-dominated landscape. Specifically, we evaluate (1) whether species richness is greater, (2) whether species trends are improved, and (3) whether species composition is more stable, across a protected area network compared to unprotected areas. We address these questions for 1238 invertebrate species based on ~1 million occurrence records across 29 years. We additionally evaluate these biodiversity metrics for pollinators and predators separately, reflecting two key ecosystem functions that invertebrates underpin - pollination and biological control respectively, as well as for rare and common species to evaluate the effectiveness of protected areas for

species of conservation concern.

2. Materials and methods

We built Bayesian occupancy-detection models for 1238 terrestrial invertebrate species (ants, bees, hoverflies, ladybirds, spiders, and wasps), based on 998044 biological records between 1990 and 2018 across Great Britain. We 'regionalized' these occupancy models (see Section 2.4 for details) based on protection status (protected or unprotected) to assess protected area effectiveness in terms of the state (species richness) and maintenance (species trends; temporal beta diversity) of biodiversity. Although our analyses were regionalized based on protection status, the underlying models estimate local (1 km scale) occupancy changes, and our analyses therefore reflect average changes in occupancy at the local scale for protected and unprotected areas across Great Britain. Our approach capitalizes on sparse unstructured data to assess multiple facets of biodiversity across the whole British protected area network, comparing biodiversity metrics for protected areas to unprotected areas - we are not, however, conducting an impact evaluation that could address what would have happened if protected areas had not been protected (Wauchope et al., 2021, 2022).

We applied our analyses overall (i.e., for all 1238 terrestrial invertebrate species), for pollinators (467 species) and predators (1018 species) (these functional groups are not mutually exclusive - see Section 2.3), and for rare (310 species) and common (310 species) species.

We used R version 4.0.1 (R Core Team, 2021) for all our analyses.

2.1. Protected areas

We extracted protected areas for Great Britain from the World Database on Protected Areas (UNEP-WCMC and IUCN, 2020). We filtered the data to terrestrial sites that are primarily designated for nature conservation and have a high level of protection, referred to by Lawton (2010) as 'tier 1 sites'. Tier 1 sites include Sites of Special Scientific Interest (SSSIs), Special Areas of Conservation (SACs), Special Protection Areas (SPAs), Ramsar Sites, National Nature Reserves (NNRs), and Local Nature Reserves (Lawton, 2010). We therefore excluded sites such as Areas of Outstanding Natural Beauty and National Parks (where these did not overlap with tier 1 sites), which are categorized as IUCN category V (protected landscape; IUCN category I is the highest protection category) (Crofts et al., 2014; Dudley, 2008; Starnes et al., 2021; Underwood et al., 2014). The selected sites are categorized as IUCN categories I-IV (stricter protection categories; Crofts et al., 2014; Dudley, 2008; Starnes et al., 2021; Underwood et al., 2014), except for Local Nature Reserves which are 'not applicable' but are primarily designated for the conservation of nature and comprise only 1 % of the total area of tier 1 sites (Lawton, 2010). SSSIs are primarily designated for their biological interest or for their geological interest or for both. We did not exclude SSSIs designated primarily for their geological interest (3 % of the total area of all SSSIs), as these sites, such as caves and waterfalls, have high levels of protection, can provide important refugia for invertebrates, and are often associated with important biodiversity and habitats (Dudley, 2008). Based on our selection criteria, 11.0 % of terrestrial Great Britain is designated as protected.

We then calculated protected area coverage per 1 km grid cell (British national grid). We defined grid cells as 'protected' if they had > 10 % protected area coverage at the start of the period (1990) and 'unprotected' if they had < 1 % protected area coverage at the end of the period (2018). The percentage thresholds we applied are commonly chosen (Andam et al., 2008; Hanauer and Canavire-Bacarreza, 2015), and ensured a clear distinction in the magnitude of protection between protected (21062 grid cells; 9 % of total [242666] grid cells) and unprotected (173270 grid cells; 71 % of total) areas (Fig. 1). We excluded 48334 grid cells (20 % of total) that did not consistently meet either of these criteria throughout the study period - i.e., cells with low protected

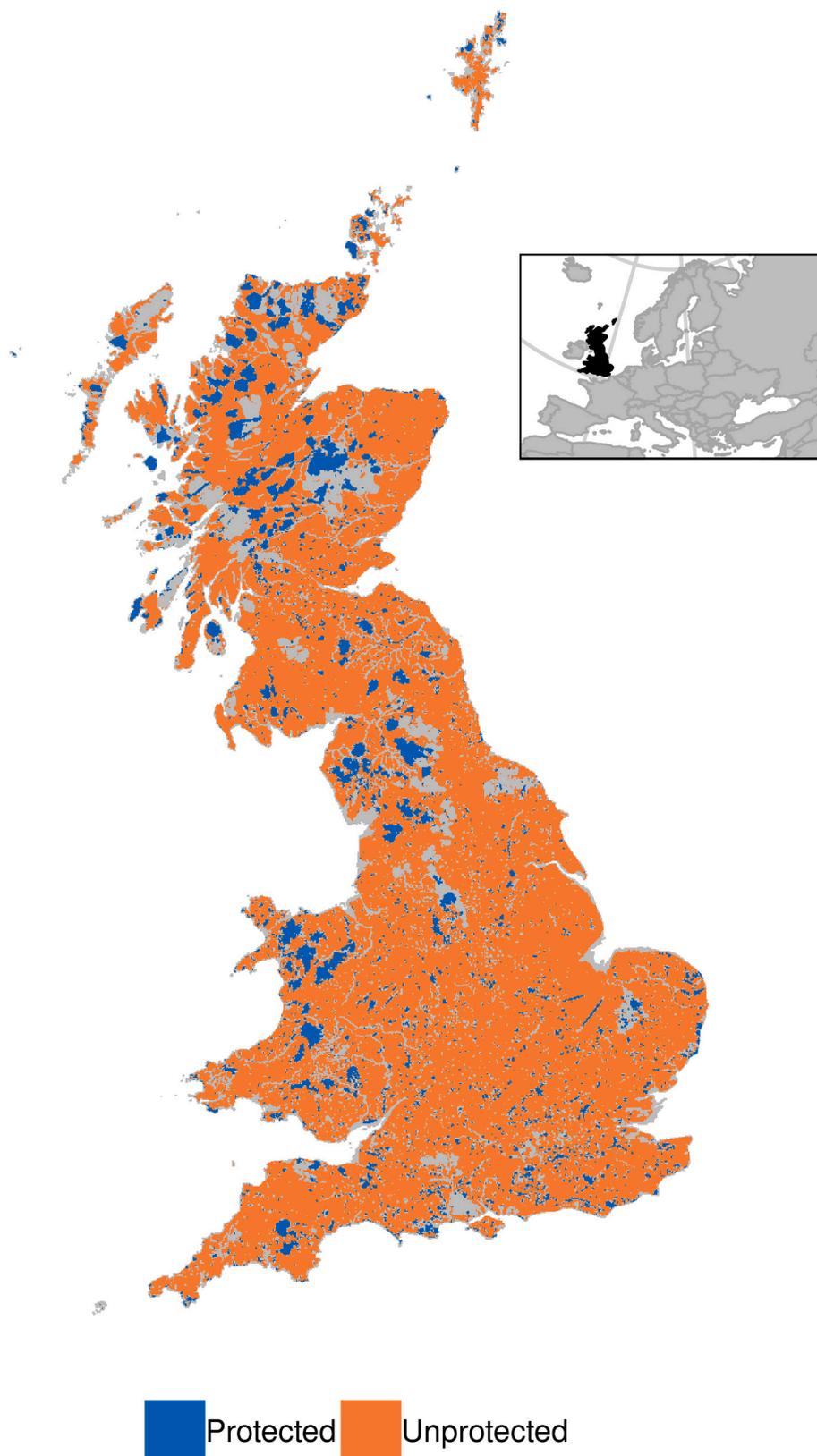


Fig. 1. Protected area status across Great Britain. 1 km grid cells (British grid) were classified as protected if $> 10\%$ of the grid cell area was designated as Tier 1 (Lawton, 2010) in 1990 (blue; 9 % of total grid cells) and as unprotected if $< 1\%$ of the cell was designated as Tier 1 in 2018 (orange; 71 % of total grid cells). Gray represents grid cells that did not meet either criterion (20 % of total grid cells). For example, grid cells where protected areas were designated after 1990, or cells with low protected area coverage (1–10 %). Inset shows the location of Great Britain within Europe (orthographic projection). Protected sites are distributed throughout the study region but occur disproportionately in the north and west of Great Britain. However, the biological records we collated (see below) were primarily from England, hence our results are more relevant to a comparison of protected and unprotected areas in England, especially southern and central England (see Section 2.5). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

area coverage (1–10 %), or cells that became protected ($> 10\%$) after 1990. Protected grid cells generally had high protected area coverage (median 1990 = 58 %; Fig. S1A in Appendix A) and most did not change in protected area coverage across the focal period (median = 0 % change; Fig. S1C in Appendix A). Still, we tested the sensitivity of the

results to this threshold for ants only (due to the computationally intense nature of the models, e.g., hoverflies took approximately two weeks to run in a high performance computing environment), comparing the $> 10\%$ threshold (21062 protected grid cells; 9 % of total grid cells) of protection to a $> 50\%$ threshold (11362 protected grid cells; 5 % of total

grid cells).

We selected 1990 as the start of the period because of (1) the greater density of biological records, and hence statistical power, after 1990 (Isaac and Pocock, 2015), (2) the majority of British protected areas had been established by 1990 (JNCC, 2021a), and (3) 1990 marks the approximate transition from land-use *change* to land-use *intensification* as the main pressure on British biodiversity (Swetnam, 2007).

2.2. Occurrence records

We collated biological occurrence records from 1990 to 2018 for six terrestrial invertebrate taxonomic groups (ants, bees, hoverflies, ladybirds, spiders, and wasps), covering 1687 native species. We used taxonomic groupings that reflect those used by British recording schemes (more information on these schemes can be found at <https://www.brc.ac.uk/recording-schemes>). We selected taxonomic groups that had recent updates from the recording schemes, high numbers of records (facilitating comparisons across protected and unprotected areas), and clear functional roles in their ecosystems (see Section 2.3; Oliver et al., 2015). We collated occurrence record data via the Biological Records Centre, Wallingford (including data from National Biodiversity Network and iRecord). Whilst providing the same information (what was seen, where, and when), the data derive from a mix of opportunistic records, checklists, inventories, mass participation events, and structured monitoring (Pocock et al., 2015), and are best described as ‘unstructured’. We cleaned the data following an established workflow (Boyd et al., 2022a; Outhwaite et al., 2019) of verification (e.g., only records verified by experts at the species level were included) and standardization (e.g., only records with date specified to day, and location at the 1 km grid cell scale were included). Hoverflies and ladybirds had the most records per species, with wasps and spiders having the fewest (Table S1 in Appendix B). The records were primarily from central and southern England (Fig. S2 in Appendix C), covering most species in most years (Fig. S5 in Appendix C), and with taxonomic groups showing variable trends in numbers of records through time (e.g., hoverflies and ladybirds showed generally increasing records through time, while spiders showed generally decreasing records through time; Fig. S6 in Appendix C).

2.3. Occupancy models

Occupancy models, when properly parameterized, represent one of the most robust methods to draw inference from unstructured biological records (Isaac et al., 2014; van Strien et al., 2013). We fit a multi-season Bayesian occupancy model (Outhwaite et al., 2018, 2019) to the occurrence records for each species. These models separate occupancy (the proportion of occupied 1 km grid cells) and detection into hierarchically coupled submodels to allow for imperfect detection and temporal changes in recorder intensity, which are common biases in occurrence record datasets (Isaac and Pocock, 2015). We used a closure period (the temporal precision of the occupancy submodel) of one year (Outhwaite et al., 2018). We therefore estimated occupancy annually between 1990 and 2018, using a separate model for each species. The detection submodel estimates the probability of detection based on repeat visits (a visit is a unique combination of 1 km grid cell and day) within years. As the data are presence-only, we used records of other species within the same taxonomic group (the target-group approach) to infer non-detections of the focal species (Kéry et al., 2010). We included the number of species recorded during a visit, categorized into lists of 1, 2–3 or 4+ records, in the detection submodel to estimate sampling intensity and variability in selective reporting (Outhwaite et al., 2019; Szabo et al., 2010; van Strien et al., 2013). We also added a random effect (intercept) of grid cell to allow for variation in occupancy status and uneven sampling among grid cells (Isaac et al., 2014; Kuussaari et al., 2007). Our models are not spatially explicit, but compare overall patterns of biodiversity between regions of protected and unprotected

areas in England (Fig. 1). Specifically, we ‘regionalized’ the occupancy models by including a term for protection status (protected or unprotected) to estimate occupancy separately for protected and unprotected areas across Great Britain, but with a common detection process (including variation in detectability among years).

For the priors, we selected a random walk prior on the year effect, which enabled the sharing of information between the current and previous year in the occupancy submodel - imposing an a priori judgement that a species’ occupancy is likely to be similar from one year to the next (Outhwaite et al., 2018, 2019). We used uninformative priors for the remaining parameters within the model, following Outhwaite et al. (2019). We did not fit models for species that we expected to produce imprecise occupancy estimates, based on data-derived thresholds described in Pocock et al. (2019). This a priori screening reduced the overall analysis to occupancy models for 1238 species, represented by 998044 occurrence records.

We fit occupancy models using the occDetFunc function in the sparta package (August et al., 2020), which uses a Markov Chain Monte Carlo algorithm to fit the models via JAGS (Plummer, 2013). We specified three chains, 32000 iterations, a burn in of 30000, and a thinning rate of six. We determined convergence based on the Gelman-Rubin statistic ($Rhat < 1.1$); the majority of species:year occupancy estimates converged (53 % of all species:year occupancy estimates converged, 55 % of first and last year estimates converged). Moreover, 86 % of species had estimates that converged in at least one year, 42 % of species had estimates that converged in both the first and last year, and 13 % of species converged in every year. For our main analyses, we retained all combinations, regardless of convergence status - the ‘full set’ (1238 species). We reasoned that poorly converged estimates are unlikely to exert directional bias on our high-level summary statistics, that it is more transparent to propagate the uncertainty associated with these species, and that removing such cases could in fact create additional biases, e.g., if models of rare species (high conservation importance) were less likely to converge. Still, the analyses have the potential to be sensitive to convergence, so we repeated these analyses with only those species with $Rhat < 1.1$ in both the first and last year - the ‘converged subset’ (520 species).

We sampled 999 samples from the posterior distribution of occupancy, for both protected and unprotected areas, per species:year combination for use in the analyses below. We therefore propagate the uncertainty from the species-specific occupancy estimates to our multi-species analyses.

2.4. Functional groups

To understand the effect of protected areas on ecosystem function provision, we classified species into functional groups (Tables S1 and S2 in Appendix B). Specifically, we classified the six taxonomic groups into predators (ants, hoverflies, ladybirds, spiders, and wasps) and pollinators (bees, and hoverflies), based on the primary ecosystem functions that these groups underpin across their lifecycle, following Oliver et al. (2015). These functions are not mutually exclusive, e.g., hoverflies provide primary contributions to both pollination and predation (Oliver et al., 2015). For predation, strictly herbivorous or fungivorous species clearly do not deliver this function and so were excluded from the analyses (five non-predatory ladybird species: *Halysia sedecimguttata*, *Henosepilachna argus*, *Psyllobora vigintiduopunctata*, *Subcoccinella vigintiquatuor punctata*, *Tytthaspis sedecimpunctata* were excluded). We acknowledge that we do not include all invertebrate species that contribute to pollination and predation, but instead select representative groups that characterise these key functions (Oliver et al., 2015; Powney et al., 2019; Schowalter et al., 2018) to generate an index of the provision of these ecological functions.

2.5. Rare vs common species

Although our main focus was on multiple broad facets of biodiversity (as protected areas should be representative of overall biodiversity, beyond just designated species; [Critchlow et al., 2022](#)), we recognize that protected areas also have a remit to support species of conservation concern ([Underwood et al., 2014](#)). Moreover, some measures of biodiversity (e.g., total species richness) can obscure the effectiveness of protected areas for species of high conservation importance ([Cazalis et al., 2020](#)). To explore this, we compared biodiversity metrics between a set of 'rare' and 'common' species. Specifically, we defined rare (i.e., localized) species (310 species) as those whose median occupancy across years was in the lower quartile (occupancy ≤ 0.03 ; equates to range size $\leq 7000 \text{ km}^2$) and common (i.e., widespread) species (310 species) as those in the upper quartile (occupancy ≥ 0.24 ; equates to range size $\geq 57000 \text{ km}^2$) ([Outhwaite et al., 2020](#)). We then repeated this comparison using a definition based on the lowest and highest deciles (i.e., 10th and 90th percentiles): very rare species (124 species; occupancy ≤ 0.008 ; equates to range size $\leq 2000 \text{ km}^2$) and very common species (124 species; occupancy ≥ 0.42 ; equates to range size $\geq 102000 \text{ km}^2$).

2.6. Risk of bias assessment

Unstructured occurrence records, as used here, can be subject to various potential biases. For instance, preferential sampling of accessible locations, or the recording of interesting (e.g., rare) species ([Isaac and Pocock, 2015](#)). Our occupancy model formulation described above attempts to mitigate potential biases, including imperfect detection, changes in sampling intensity, and selective reporting. Still, it is useful to understand the potential for bias in our data, so that our results may be interpreted appropriately. Hence, we performed a ROBITT ([Boyd et al., 2022b](#)) assessment (Appendix C). We used the `assessSpatialBias`, `assessSpatialCov`, and `assessSpeciesNumber` functions from the `occAssess` package ([Boyd, 2022](#); [Boyd et al., 2021](#)) to quantify and visualize heuristics of spatial bias and coverage.

Our ROBITT assessment highlights the unstructured nature of our occurrence record data. Overall, risk of spatial bias was generally quite low (Fig. S1 - Appendix C), however risk of spatiotemporal bias was relatively high (most grid cells were sampled in a relatively low proportion of years), although generally reflecting local shifts in sampling within the focal period (between 1 km grid cells but within 10 km grid cells; Figs. S3 and S4 - Appendix C). Taxonomic coverage was relatively good across most years, especially for the functional groups applied here (Fig. S5 - Appendix C), and repeat visits (grid cells that were visited more than once within a year) showed good temporal coverage (Fig. S6 - Appendix C). Still, after assessing the risk of bias, we note that our results are more relevant to a comparison of protected and unprotected areas in England, especially southern and central England (Figs. S2 and S3 - Appendix C), rather than being truly representative of Great Britain as a whole, and that our overall trends in occupancy are likely to be more informative than our annual estimates of occupancy.

2.7. Species richness

To quantify species richness (average species richness per grid cell for each protection status) we summed species' occupancy per year ([Dorazio et al., 2006](#)). We summarized species richness for the focal period with the arithmetic mean of species richness across years. We then calculated an absolute effect size as the median difference, with 95 % credible interval using the `HDInterval` function (`hdi` package; [Meredit and Kruschke, 2018](#)), of species richness between protected and unprotected areas. We also calculated Hedge's *g*, with 95 % confidence interval, as a measure of relative effect size via the `cohen.d` function (`effsize` package; [Torchiano, 2016](#)). As an example, a Hedge's *g* of one indicates that protected and unprotected areas differ by one standard deviation.

2.8. Species trends

We calculated multispecies composite trends for each group (overall, predators, and pollinators) for the protected and unprotected 'regions' through time. Specifically, we calculated geometric mean occupancy across species within each functional group per region per year, propagating uncertainty from the species-specific models and summarizing these data as the median and 95 % credible intervals for each group: region:year combination.

We also summarized species trends as the percentage annual growth rate of occupancy (hereafter growth rate) ([Outhwaite et al., 2019](#)) between the first (1990) and last (2018) years of data:

$$\text{growth rate} = \left(\left(\frac{f}{s} \right)^{\frac{1}{y}} - 1 \right) \times 100$$

where *f* was occupancy in the final year, *s* was occupancy in the starting year, and *y* was the number of years. We then calculated absolute (median difference) and relative (Hedge's *g*) effect sizes with their associated uncertainty as above.

2.9. Temporal beta diversity

We also calculated temporal beta diversity ([Legendre, 2019](#)). Temporal beta diversity summarizes compositional change through time ([Magurran et al., 2019](#)) and therefore relates to processes that support and maintain biodiversity ([Kraft et al., 2011](#)). In addition, unlike species richness and species trends, temporal beta diversity takes into account the identities of species ([Baselga and Orme, 2012](#)), and therefore reflects biodiversity changes in relation to species identity. We quantified temporal beta diversity using *occupancy* similarity in place of *abundance* similarity ([Xu et al., 2015](#)).

We calculated temporal beta diversity ([Legendre, 2019](#)) between 1990 and 2018, which reflects the total dissimilarity in species occupancy for protected and unprotected areas through time. High values of temporal beta diversity therefore relate to strong compositional change, and consequently low compositional stability ([Donohue et al., 2013](#)). We also decomposed temporal beta diversity into occupancy-per-species losses (i.e., local extinction) and occupancy-per-species gains (i.e., local colonization), which reflect the ecological processes that shape and reorganize invertebrate communities. To note - total temporal beta diversity is the sum of losses and gains, high temporal beta diversity therefore reflects *both* high losses and high gains (i.e., magnitude of change, not net change). We also reported net change (gains minus losses) to aid interpretation, with positive change values indicating net gain and negative values indicating net loss. We calculated temporal beta diversity for protected and unprotected areas, based on the Bray-Curtis dissimilarity index, with the TBI function (`adespatial` package; [Dray et al., 2019](#)). As above, we calculated absolute and relative effect sizes.

3. Results

3.1. Species richness

Terrestrial invertebrate species richness is greater in protected areas than unprotected areas (Fig. 2). The average protected grid cell contains 229 species (95 % credible interval: 226, 233; species pool = 1238 invertebrate species) and the average unprotected grid cell 200 species (197, 203). In other words, protected areas harbour 15 % (13, 16) more invertebrate species on average than unprotected areas. We see similar results for the converged subset (i.e., excluding models that did not converge; Fig. S1A in Appendix D). In addition, results are qualitatively similar when defining protected cells based on either a > 10 % or > 50 % protected area coverage threshold (for ants only due to computational cost; Fig. S2 in Appendix D). Thus, across Great Britain, protected areas

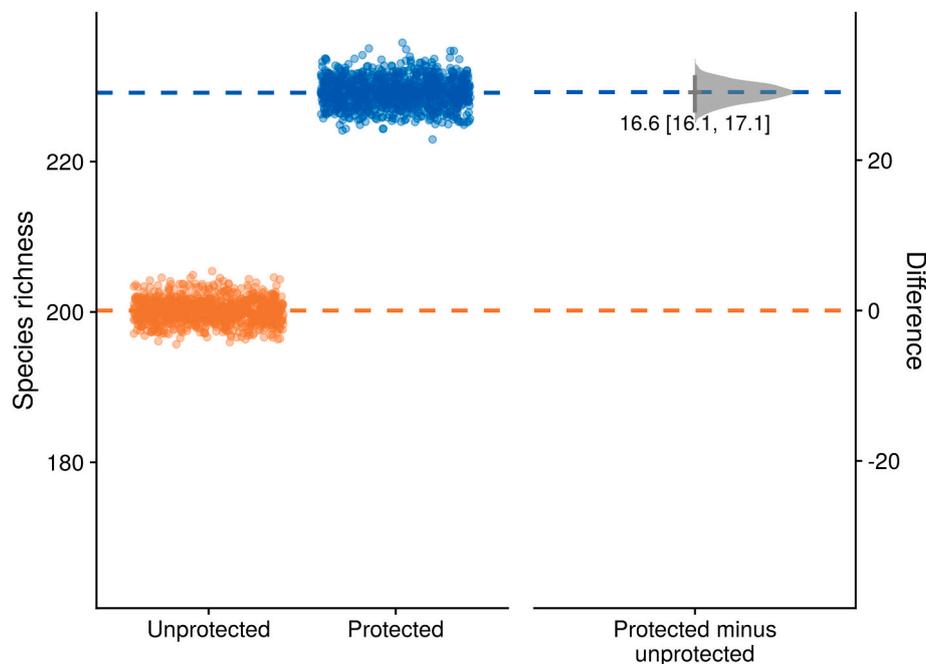


Fig. 2. Species richness in protected and unprotected areas for 1238 terrestrial invertebrate species across Great Britain. Plot elements: points show 999 posterior estimates per group with dashed lines indicating medians. The difference (protected minus unprotected) is then shown on the right with median, 95 % credible interval, and the density distribution. The relative effect size with 95 % confidence interval is reported per panel.

have greater species richness than unprotected areas.

3.2. Species trends

Since 1990, invertebrates have declined overall in both protected (median growth rate = -0.5 % per year: -0.6 , -0.3) and unprotected (-0.4 % per year: -0.6 , -0.3) areas (Fig. 3). These overall declines reflect fluctuating increases in occupancy up to ~ 2006 , before a decline to levels below those of 1990 (Fig. 3A). Although there is some variation, trends are broadly mirrored between protected and unprotected areas (Fig. 3A), although with slightly greater declines for protected areas (Fig. 3B). However, these differences are small compared with the uncertainty. The median difference in growth rates between protected and unprotected areas is -0.0 (-0.2 , $+0.2$; 68 % of the posterior distribution lies below zero and 32 % above; Fig. 3B). Hence, in contrast to species richness, we find that species occupancy trends are no better in protected areas compared to unprotected areas (Fig. 3). These results are generally reflected for the converged subset (Fig. S1B in Appendix D).

3.3. Temporal beta diversity

On average, invertebrate species composition has changed 27 % (26, 28) between 1990 and 2018 in both protected and unprotected areas (Fig. 4A). Occupancy-per-species losses (16 %: 15, 17, for protected areas and 15 %: 14, 16, for unprotected areas; Fig. 4B), slightly outweighed occupancy-per-species gains (11 %: 11, 12, for protected areas and 12 %: 12, 13, for unprotected areas; Fig. 4C). The difference in total temporal beta diversity between protected and unprotected areas is effectively zero (Fig. 4A). However, we find evidence of greater losses (96 % of the posterior distribution lies above zero; Fig. 4B) and fewer gains (97 % of the posterior distribution lies above zero; Fig. 4C) across protected areas compared to unprotected areas. Hence net loss (gains minus losses) is more severe for protected areas at -4.5 % (-5.7 , -3.2) than unprotected areas at -2.5 % (-3.8 , -1.1). These net losses in occupancy-per-species translate to the average loss of approximately 10 (7, 13) species per grid cell between 1990 and 2018 across protected areas and 5 (2, 8) species for unprotected areas. Still, the differences

(absolute effect sizes) are relatively small (both ~ 1 %; median difference in losses = $+1.1$ %: -0.1 , $+2.1$; median difference in gains = -0.9 %: -2.0 , -0.0 ; Fig. 4B,C), considering the 29 year timeframe. Temporal beta diversity for the converged subset generally shows agreement (Fig. S1D-F in Appendix D), although with similar (rather than fewer) gains in both protected and unprotected areas (Fig. S1F in Appendix D).

3.4. Functional groups - predators and pollinators

We also quantified the difference in biodiversity between protected and unprotected areas for predators (1018 species; ants, hoverflies, ladybirds, spiders, and wasps) and pollinators (467 species; bees, and hoverflies) separately. Predators generally reflect the overall results (compare Figs. 2-4 to Fig. S3 in Appendix D). By contrast, pollinators show deviations from the overall results (compare Figs. 2-4 to Fig. 5). Pollinators have suffered particularly severe declines in occupancy (protected areas median growth rate = -0.7 % per year: -0.9 , -0.4 ; unprotected areas median growth rate -0.8 % per year: -1.0 , -0.5), especially since 2006, with weak evidence (80 % of the posterior distribution lies above zero) that these declines are less severe in protected areas (Fig. 5B,C). In addition, we see greater gains across protected areas compared to unprotected areas for pollinators (median difference in gains = $+1.7$ %: $+0.5$, $+2.7$; > 99 % of the posterior distribution lies above zero; Fig. 5F). Hence protected areas show lower net losses in occupancy-per-species compared to unprotected areas between 1990 and 2018 (protected areas net change = -3.8 %: -5.4 , -2.3 ; unprotected areas net change = -5.8 %: -7.3 , -4.3 ; Fig. 5E,F). Protected areas therefore play a potentially important role for wild pollinator diversity.

3.5. Rare vs common species

We see contrasting results for rare and common species. Again, we see greater species richness in protected areas compared to unprotected areas for both rare (Fig. 6A) and common (Fig. 6B) species, with almost double ($1.7\times$: 1.2, 2.4) the number of rare species in protected areas (8.4 : 7.2, 9.6 species for the average protected grid cell vs 5.0 : 4.1, 6.2

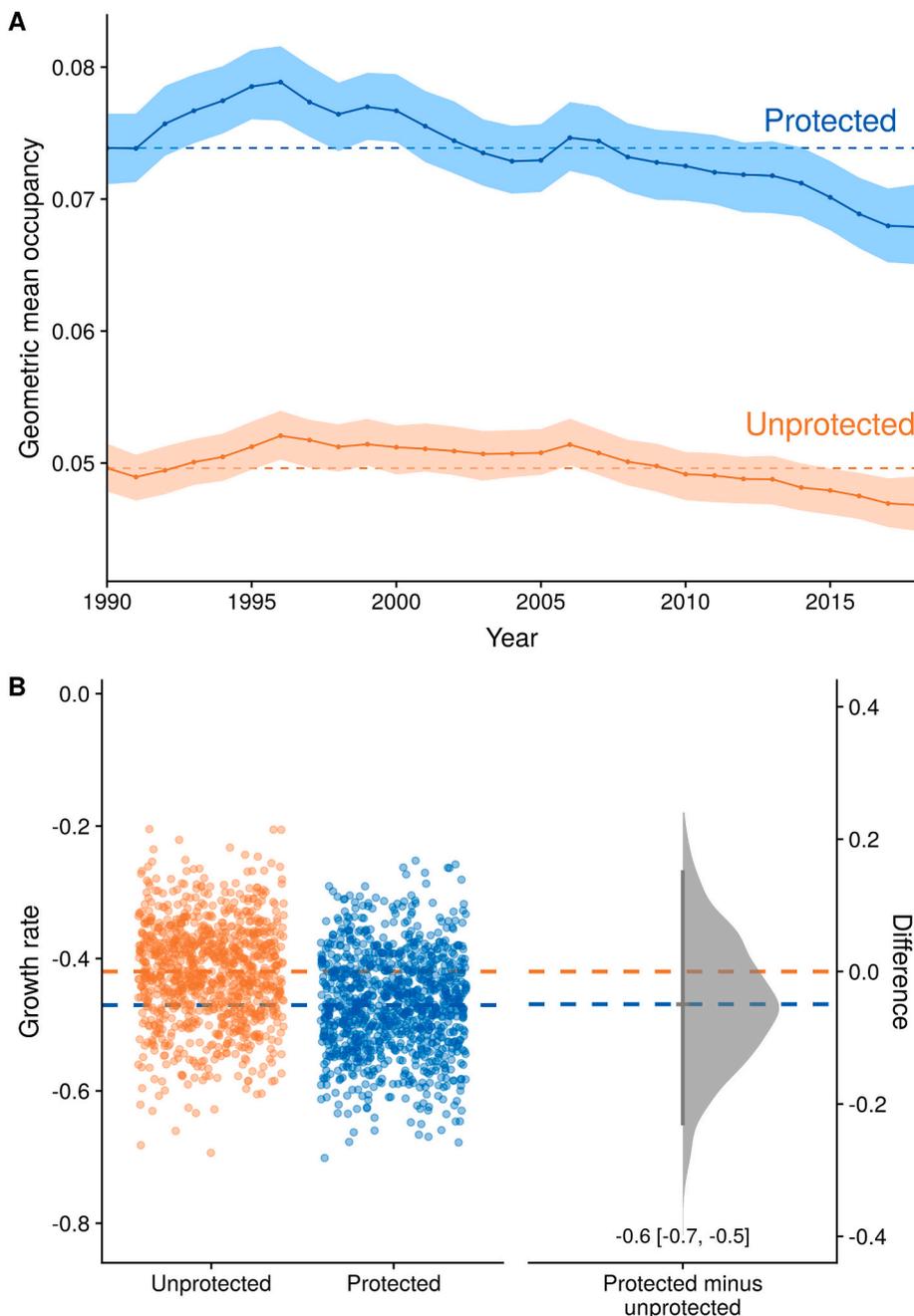


Fig. 3. Trends and growth rates in protected and unprotected areas for 1238 terrestrial invertebrate species across Great Britain. (A) Multispecies distributional trends show geometric mean occupancy, with 95 % credible intervals (shaded envelopes); dashed lines indicate occupancy in the first year. Our ROBITT assessment highlights that the overall trends presented here are likely to be more representative than the specific annual estimates of occupancy (Appendix C). (B) Growth rates with the difference between protected and unprotected areas; plot elements as in Fig. 2. Growth rates are measured in units of percentage change per year on average.

species for the average unprotected grid cell; rare species pool = 310 species; Fig. 6A). Yet, for rare species we see approximately stable trends (subtle increases based on geometric mean occupancy, Fig. 6C; subtle decreases based on median growth rate, Fig. 6E) across both protected and unprotected areas. In addition, we find similar compositional change across protected and unprotected areas for rare species (Fig. 6G, I, K). Thus, we do not find a clear difference between protected and unprotected areas for rare species (Fig. 6E, G, I, K). By contrast, we find steeply declining trends for common species, especially in protected areas (Fig. 6D, F). As well as greater occupancy-per-species losses in protected areas compared to unprotected areas for common species (Fig. 6J), resulting in greater net loss of common species in protected areas (protected areas net change = -6.1% : -7.6 , -4.4 ; unprotected areas net change = -4.0% : -5.7 , -2.6). Thus, we highlight the disproportionate loss of common species from protected areas. Results for very rare and very common species were in line with these results

(Fig. S4 in Appendix D).

4. Discussion

Protected areas are designed to “achieve the long-term conservation of nature” (UNEP-WCMC et al., 2020), yet assessments of their effectiveness at maintaining biodiversity through time are scarce (Rodrigues and Cazalis, 2020). Poor understanding of the effectiveness of protected areas exposes them to criticism or degazettement (Mascia and Paillet, 2011; Maxwell et al., 2020). Here, using occupancy-detection models, we analyse observational records for under-studied, but ecologically important, invertebrate species across both the state of biodiversity (species richness) and its maintenance through time (species trends, changes in composition). Overall, we show that although invertebrate species richness is greater in protected areas compared to unprotected areas across Great Britain, species distributional trends and

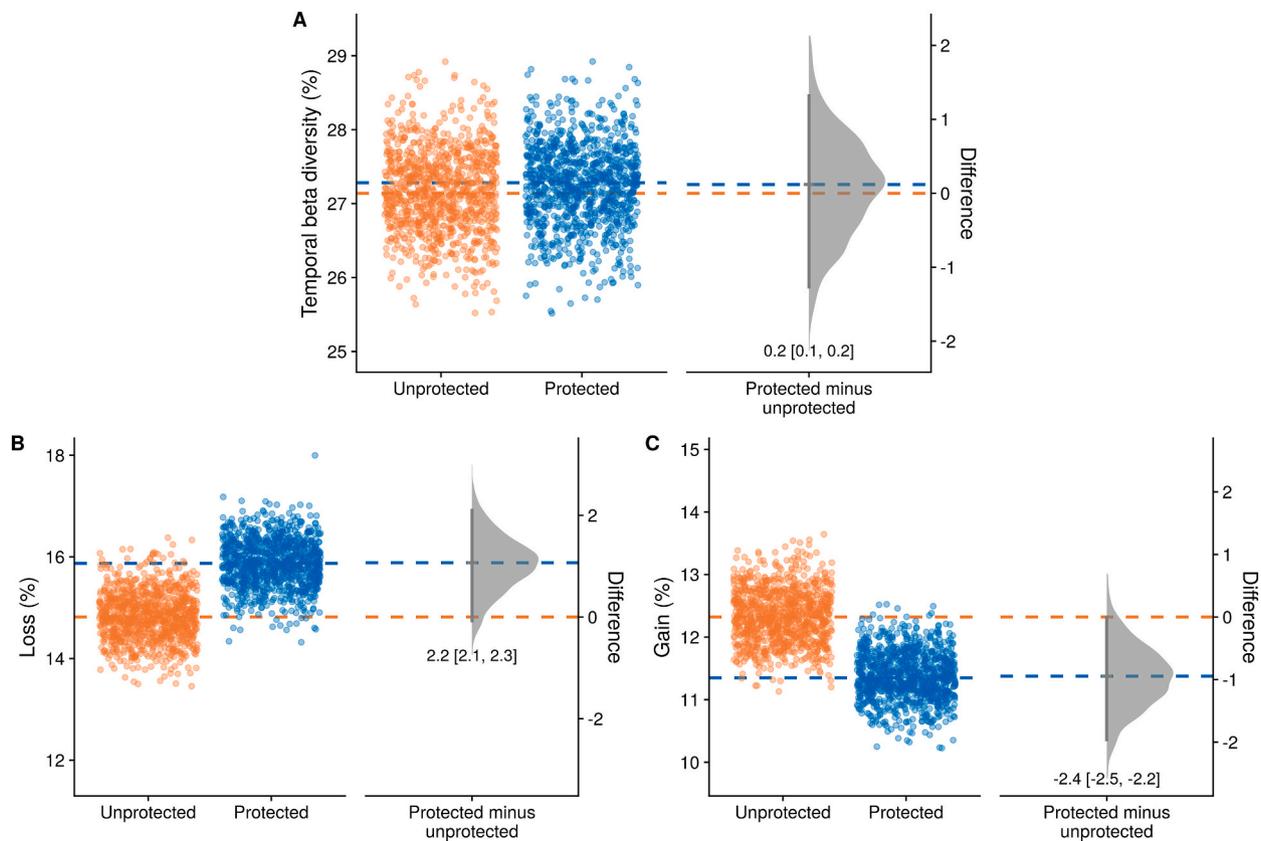


Fig. 4. Differences in occupancy-based temporal beta diversity between protected and unprotected areas for 1238 terrestrial invertebrate species across Great Britain between 1990 and 2018. (A) Total temporal beta diversity (%) is partitioned into (B) occupancy-per-species loss and (C) occupancy-per-species gain; plot elements as in Fig. 2.

compositional change are often similar across protected and unprotected areas, although precise patterns vary across functional groups.

We add further evidence of greater species richness in protected areas compared to unprotected areas (Gray et al., 2016). Existing evidence is particularly strong in temperate regions, with mixed evidence in the tropics (Cazalis et al., 2020; Coetzee et al., 2014; Gray et al., 2016). Here we extend the finding of greater species richness in temperate protected areas for key functional groups - invertebrate pollinators and predators. The greater species richness within these functional groups has the potential to insure ecosystem functions against environmental change and disturbance (Oliver et al., 2015; Yachi and Loreau, 1999). We suggest two potential explanations for the finding of greater species richness in protected areas. First, it could be due to the effective placement of protected areas across Great Britain - capturing areas of high biodiversity (including here for invertebrates, which are rarely the primary focus when designating these sites). This explanation is supported by previous analyses that have observed high species representativeness for British protected areas (Critchlow et al., 2022; Cunningham et al., 2021; Hopkinson et al., 2000; Rodrigues et al., 1999). Second, we might observe greater species richness in protected areas due to greater historic (pre-1990) losses across unprotected areas. Indeed, based on long-term structured abundance data it is clear that some groups that primarily occupy unprotected sites, such as farmland birds, have shown greater rates of decline prior to 1990, with more moderate declines since then (JNCC, 2021b).

We also contribute to an emerging, and concerning, evidence base, which suggests that protected areas are equally susceptible to biodiversity declines as unprotected areas (Rada et al., 2019; Wauchope et al., 2022). We identify declines overall for invertebrates, and particularly for pollinators, of similar magnitude across protected and unprotected areas. We therefore add a further case to worrying examples of

biodiversity declines within protected areas (Craigie et al., 2010; Hallmann et al., 2017; Rada et al., 2019; Wauchope et al., 2022). Moreover, we set these declines against the yardstick of unprotected areas. Without this comparison we cannot know whether these declines within protected areas (Craigie et al., 2010; Hallmann et al., 2017) are less than, equal to, or greater than those outside of protected areas. More formally, the 'impact' of protection (i.e., what would have happened in the absence of protection) can only be evaluated if more strict data/methodological requirements are met (e.g., matched counterfactuals are available, data are available both before and after a protected area was designated) (Jellesmark et al., 2021; Wauchope et al., 2022). Instead, we show that protected areas are performing no better than unprotected areas across Great Britain. Clearly, declines within protected areas, especially when these are equivalent to those occurring in unprotected areas, indicate that protected areas are ineffectively conserving biodiversity.

Assessments of the effectiveness of protected areas typically focus on species richness (Cazalis et al., 2020; Coetzee et al., 2014; Gray et al., 2016), whilst beta diversity has received much less attention (although see Hiley et al., 2016). Yet, temporal beta diversity can provide more information content (than species richness alone) on biodiversity change, as it reflects how aspects of composition such as dominance and identity shift over time (Hillebrand et al., 2018; Magurran et al., 2019). Even if there is no change in species richness there can be major compositional reorganization (Hillebrand et al., 2018). Indeed, compositional change is emerging as a potential signature of local biodiversity change (Dornelas et al., 2014; Dornelas and Madin, 2020). Moreover, these changes are often non-random, with a few winners (generalist, common, non-threatened and/or human-tolerant species) replacing many losers (specialist, rare, threatened and/or human-sensitive species), resulting in biotic homogenization (Cazalis, 2022;

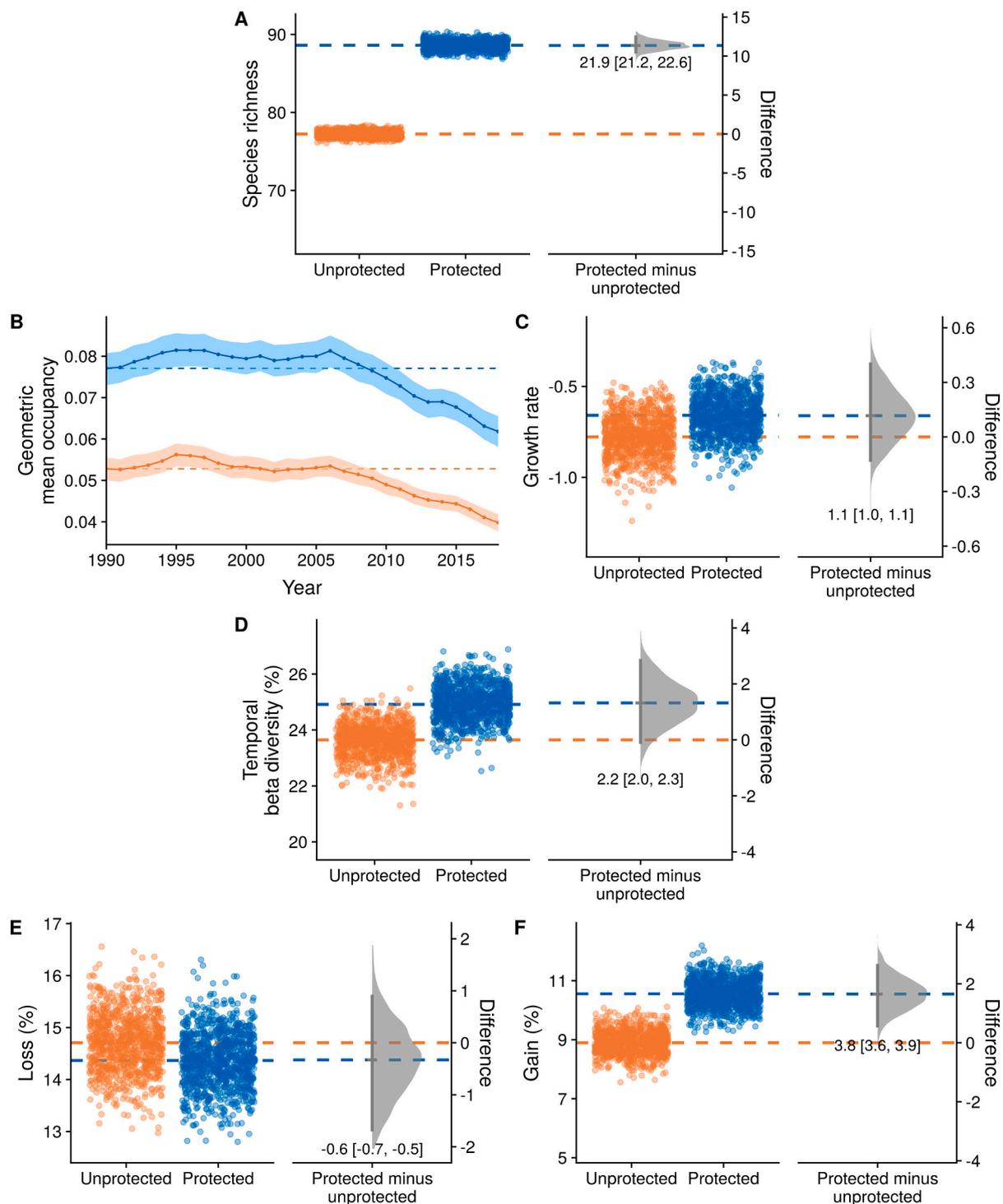


Fig. 5. Biodiversity metrics for protected and unprotected areas for 467 pollinator species across Great Britain. (A) Species richness (see Fig. 2), (B) multispecies trends (see Fig. 3), (C) growth rates (see Fig. 3), and (D) temporal beta diversity, (E) occupancy-per-species loss and (F) occupancy-per-species gain (see Fig. 4).

Clavel et al., 2011; McKinney and Lockwood, 1999). Here, we find that British protected areas show similar levels of total compositional change through time as unprotected areas. In fact, species composition has changed 27 % across both protected and unprotected areas, with losses dominating gains, suggesting strong biological, and likely functional, reorganization. Worryingly, we find evidence of greater net loss for protected areas compared to unprotected areas. Thus, although average species trends are declining similarly in both protected and unprotected areas, these declines are likely associated with specific species in protected areas. In fact, contrary to previous findings (Cazalis, 2022; Clavel

et al., 2011), for British protected areas we find the greatest losses for common species. Hence, we add further support for the need to conserve common species across protected area networks (Devictor et al., 2007). Indeed, conserving common species can help to maintain their associated ecosystem functions (Gaston, 2010; Lindenmayer et al., 2011), where common species contribute much of the structure, biomass, and energy turnover within ecosystems (Gaston, 2010).

These invertebrate losses could also be related to the ‘protection paradox’ (Bates et al., 2019) - protected areas can mitigate against some pressures, such as habitat loss, road expansion, and urban encroachment

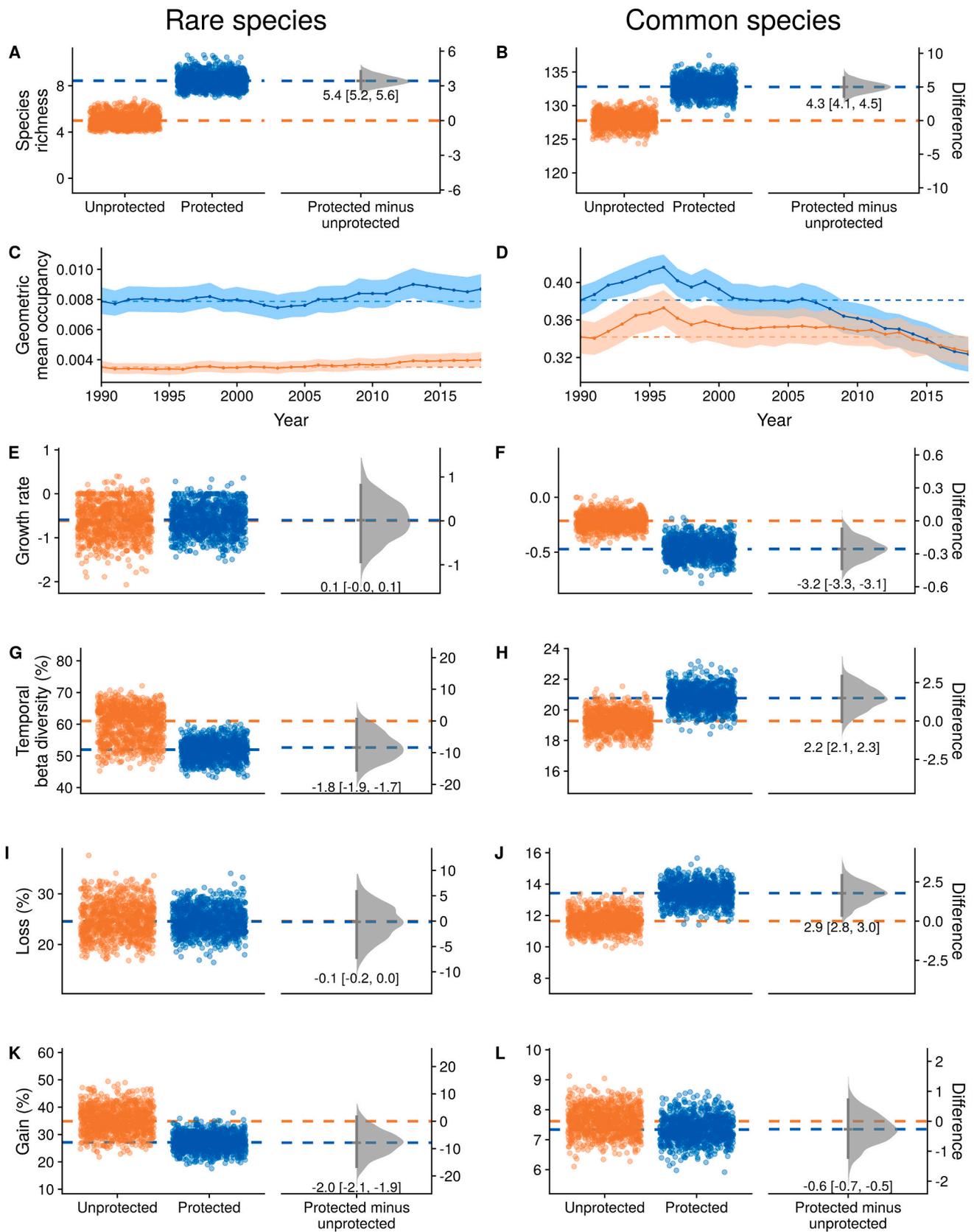


Fig. 6. Biodiversity metrics for protected and unprotected areas for rare (i.e., localized) and common (i.e., widespread) species. Species were defined based on occupancy as rare (lower quartile; occupancy ≤ 0.03 ; equates to range size $\leq 7000 \text{ km}^2$; 310 species) and common (upper quartile; occupancy ≥ 0.24 ; equates to range size $\geq 57000 \text{ km}^2$; 310 species). (A,B) Species richness (see Fig. 2), (C,D) multispecies trends (see Fig. 3), (E,F) growth rates (see Fig. 3), and (G-L) temporal beta diversity (see Fig. 4).

(Geldmann et al., 2013; Laurance et al., 2012), but this can lead to the retention of more sensitive (e.g., rare) species that are highly vulnerable to other, more pervasive pressures, such as climate change, human disturbance, disease, and pollution (Geldmann et al., 2014, 2019; Jones et al., 2018; Laurance et al., 2012). We do indeed find almost double the number of rare species for protected areas compared to unprotected areas, suggesting that protected areas may have retained more rare species under historic (pre-1990) pressures. However, we do not find that these rare species are disproportionately suffering under recent pressures, with approximately stable trends – potentially reflecting the ‘ski-jump effect’ (a major decline is followed by a stable period at a depressed level; Sadovy de Mitcheson et al., 2020). We also suggest that the losses we identify for protected areas could be driven by shortfalls in protected area funding and management (Gill et al., 2017; Starnes et al., 2021) and/or from habitat deterioration in the wider landscape. For instance, habitat changes in unprotected areas could leave protected areas more isolated, with smaller (meta-)populations, and therefore potentially unable to sustain viable populations (Armsworth et al., 2011; Schwartz et al., 2017), leading to the accumulation, and realization of, extinction debts (Lira et al., 2019). Overall, accelerating environmental change, including pervasive threats (i.e., those that also occur in protected areas), are likely driving changes to the structure, composition, and function of invertebrate communities across Great Britain.

Predatory invertebrates generally reflect the overall results, however pollinators show some specific patterns. Worryingly, pollinators suffered severe distributional declines across both protected and unprotected areas, especially since 2006, adding more evidence to previous concerns (Biesmeijer et al., 2006; Potts et al., 2010; Powney et al., 2019). These pollinator declines likely result in the loss of pollination services, which has repercussions for the maintenance of wild plant diversity, wider ecosystem stability, agricultural crop production, and food security (Ollerton et al., 2011; Potts et al., 2010). Yet we find that the effect of protection is particularly beneficial for pollinators, with much greater species richness and reduced net losses in occupancy compared to unprotected areas. Indeed, although occupancy losses dominate gains for pollinators (i.e., more pollinator ranges are shrinking than expanding), we find greater gains in protected areas compared to unprotected areas. Protected areas may therefore act as ‘landing pads’ for range-shifting pollinators and then as ‘establishment centres’ from which viable populations spread (Hiley et al., 2013). Thus, protected areas appear to provide more opportunities for pollinators to colonise and expand their ranges, highlighting the importance of protected areas for pollinators.

Protected areas are designated and managed based on a range of different criteria and objectives, including diversity, rarity, important habitats, or key species (JNCC, 2019; Ratcliffe, 1977; Underwood et al., 2014). We did not assess each protected area against their specific designation types (e.g., SSSIs, SACs, SPAs, NNRs) and management objectives, instead we evaluated the overall effectiveness of the British protected area network for multiple facets of invertebrate biodiversity. By contrast, across Great Britain the Joint Nature Conservation Committee (JNCC) assesses some protected areas (SSSIs, SACs, and SPAs) against the condition of designated features (JNCC, 2004; Starnes et al., 2021). For instance, the monitoring protocol assesses the condition of management units or designated features as ‘favourable’, ‘unfavourable’, ‘partially destroyed’ or ‘destroyed’. Additionally, a trend indicator of ‘maintained’, ‘recovered’, ‘recovering’, ‘no change’ or ‘declining’ may be applied (JNCC, 2004; Starnes et al., 2021). The JNCC assessments show that the majority of these protected areas (49–57 %) are in unfavourable condition (including unfavourable recovering; 27–35 %) or worse, adding evidence that protected areas are underperforming for designated species and habitats (Starnes et al., 2021). These are complementary strands of evidence, as individual protected areas need to meet their specific objectives, but this should not come at the cost of overall negative effects on biodiversity across the protected area network. A protected area network should be representative of

overall biodiversity, beyond just designated species (Critchlow et al., 2022). Our framework compliments these existing condition-based assessments (Starnes et al., 2021), and could be taxonomically expanded and regularly applied to quantify trends in the performance of the British protected area network - filling a need for a direct indicator of protected area effectiveness (Bailey et al., 2022). Indeed, our approach provides a toolkit for assessing the effectiveness of a protected area network, or any site based conservation intervention, and could be applied in any region with sufficient biodiversity monitoring, even when only unstructured datasets are available. Moreover, our results provide a baseline against which to assess performance of protected areas in the future, both in Britain and elsewhere.

Conservationists have the opportunity to address ineffective protected areas. For instance, examples of successful species-level interventions are not common but do exist (Bane et al., 2022; Bolam et al., 2021), including for invertebrates, such as the Large Blue Butterfly *Phengaris arion* (Thomas et al., 2011) and Fen Raft Spider *Dolomedes plantarius* (Bane et al., 2022). Still, these species-specific actions (including breeding programs, translocations, reintroductions, legal protection, targeted habitat management, and tailored agri-environment schemes; Bane et al., 2022) should be set in the context of wider biodiversity and ecosystem conservation, including supporting common, but declining, species (Devictor et al., 2007; Lindenmayer et al., 2011). Although we acknowledge the difficulty of this in the face of pervasive human-driven pressures, including the accelerating effects of climate change. Protected areas require both appropriate management and regular monitoring to be effective (Leverington et al., 2010; Tanner-McAllister et al., 2017; Watson et al., 2014). Here, we use monitoring data to provide a broad perspective across the protected area network. However, improved site-level monitoring data could help to assess the effectiveness of individual protected areas (building on condition-based assessments; JNCC, 2004; Starnes et al., 2021) and provide managers with the knowledge to leverage change. For example, monitoring data could reveal the need to restore habitat that has lost previously occurring species (local extirpation) before they are lost more widely (regional extirpation/extinction). Moreover, greater knowledge of biodiversity change (at both the site and network scale) as it occurs could help to improve and adapt management regimes (Waylen et al., 2019), which is likely to be crucial in a changing world (Tanner-McAllister et al., 2017). For example, adaptive management could be implemented to allow the successful colonization of protected areas by range-shifting species under climate change (Hiley et al., 2013; Tanner-McAllister et al., 2017). Improved biodiversity monitoring requires a diverse and integrated monitoring network (Kühl et al., 2020; Navarro et al., 2017) that captures multiple biodiversity facets (e.g., abundance, species richness, beta diversity, functional diversity), with potential for automated approaches (van Klink et al., 2022). This monitoring network could facilitate and improve multi-scale, from individual protected areas to protected area networks, assessments of protected area effectiveness, directly informing management decisions.

The invertebrate declines we identify highlight the need for broad-scale invertebrate conservation and threat mitigation (Harvey et al., 2020; Wagner, 2020). Across Great Britain, initiatives such as ‘30 by 30’ (Bailey et al., 2022; UK Government, 2020), the reform of environmental land management schemes (Redhead et al., 2022; UK Government, 2020), landscape conservation, e.g., the Wildlife Trusts’ ‘Living Landscapes’ (Wildlife Trusts, 2009), and corridors to improve the quality and extent of landscape connectivity (Isaac et al., 2018; Lawton, 2010) could provide opportunities to build a more effective and resilient network for nature. Specifically, above we highlight the need for better maintenance of common, but declining, species; greater action to slow and reverse wild pollinator declines; appropriate species- and landscape-scale conservation actions; and continual assessments of the condition and effectiveness of protected areas. More widely, we require increased efforts, beyond those listed here, to meet the vision set out by the Convention on Biological Diversity for biodiversity to be ‘valued,

conserved, restored and wisely used, maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people' by 2050 (Convention on Biological Diversity, 2020). Overall, we highlight the need for *effective* protected areas, in combination with conservation action across the wider landscape, to bend the curve of biodiversity loss.

4.1. Conclusions

Protected area goals need to move beyond simplistic coverage-based metrics and consider the effectiveness of protected areas at conserving the state of biodiversity and its maintenance through time (Barnes et al., 2018; Ralimanana et al., 2022; Rodrigues and Cazalis, 2020). We highlight the greater terrestrial invertebrate species richness of British protected areas and its importance for biodiversity. Yet our evidence also suggests that invertebrates are ineffectively conserved through time with distributional declines and biological, and functional, reorganization identified - both within and outside protected areas. Thus, although protected areas are a cornerstone of conservation, we require protected areas to effectively conserve biodiversity through time to fulfil their remit.

Data statement

The raw data used in the analyses were provided by multiple recording schemes (Bees, Wasps and Ants Recording Society, the Hoverfly Recording Scheme, the UK Ladybird Survey, and the Spider Recording Scheme) via the Biological Records Centre (BRC), Wallingford (<https://www.brc.ac.uk/>). Data requests should be directed to the BRC. The R code and processed data for the occupancy models and statistical analyses are available online at https://github.com/03rcooke/pa_occ.

CRediT authorship contribution statement

Rob Cooke: Conceptualization, Methodology, Software, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Francesca Mancini:** Software, Formal analysis, Data curation, Writing – review & editing. **Robin J. Boyd:** Methodology, Writing – review & editing. **Karl L. Evans:** Conceptualization, Methodology, Writing – review & editing. **Anna Shaw:** Conceptualization, Methodology. **Thomas J. Webb:** Conceptualization, Methodology, Writing – review & editing. **Nick J.B. Isaac:** Conceptualization, Methodology, Writing – review & editing, Project administration, Funding acquisition.

Declaration of competing interest

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

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109884>.

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