ARTICLES
https://doi.org/10.1038/s41559-020-1111-z

nature ecology & evolution

Complex long-term biodiversity change among invertebrates, bryophytes and lichens

Charlotte L. Outhwaite[1,2,3]*, Richard D. Gregory[2,3], Richard E. Chandler[4], Ben Collen[2,5] and Nick J. B. Isaac[1]

Large-scale biodiversity changes are measured mainly through the responses of a few taxonomic groups. Much less is known about the trends affecting most invertebrates and other neglected taxa, and it is unclear whether well-studied taxa, such as vertebrates, reflect changes in wider biodiversity. Here, we present and analyse trends in the UK distributions of over 5,000 species of invertebrates, bryophytes and lichens, measured as changes in occupancy. Our results reveal substantial variation in the magnitude, direction and timing of changes over the last 45 years. Just one of the four major groups analysed, terrestrial non-insect invertebrates, exhibits the declining trend reported among vertebrates and butterflies. Both terrestrial insects and the bryophytes and lichens group increased in average occupancy. A striking pattern is found among freshwater species, which have undergone a strong recovery since the mid-1990s after two decades of decline. We show that, while average occupancy among most groups appears to have been stable or increasing, there has been substantial change in the relative commonness and rarity of individual species, indicating considerable turnover in community composition. Additionally, large numbers of species have experienced substantial declines. Our results suggest a more complex pattern of biodiversity change in the United Kingdom than previously reported.

The large-scale study of the state of biodiversity is key to ensuring that conservation actions are targeted appropriately. However, high-quality population time series collected annually are typically restricted to birds[1], other vertebrates[2] and butterflies[3,4]. Most invertebrates do not feature in studies of large-scale biodiversity trends[2,5], and it is unclear whether these well-studied groups reflect changes in wider biodiversity[6–8]. Invertebrates and plants constitute a substantial portion of biodiversity and support many ecosystem functions, so their lack of representation could mean that important trends are being overlooked. Recent concern about the status of understudied groups, particularly insects[9–12], has been echoed by concerns about the quality of available evidence[13,14]. There is thus an urgent need to mobilize existing data and interrogate them with modern, rigorous analysis tools.

Here, we explore long-term changes in UK biodiversity through an analysis of changes in the annual occupancy of numerous invertebrate groups, bryophytes and lichens. The United Kingdom is relatively well monitored in terms of national-scale species' status and trends for some taxa[15,16]. The farmland bird index has declined by over 50% since 1970[17], the abundance of specialist butterflies fell by 45% from 1976 to 2014[18] and vascular plant communities have declined, largely in response to nitrogen deposition[19]. Conversely, bat populations in Great Britain have generally shown stable or positive trends since the late 1990s[20]. The estimation of these trends has been possible through the standardized collection and analysis of abundance data. Equivalent knowledge is lacking for most taxa, particularly invertebrates. However, owing to the rich history of species observation and recording across the United Kingdom that goes back many decades[21], extensive occurrence data are available for these groups in the form of biological records. A record is simply a report of a species by an observer at a known time and place; most are collected opportunistically. These data have been underused because of concerns over biases resulting from the unstandardized nature of the data collection[22–24]. Here, we use recent advances in occupancy modelling techniques that address these concerns and have enabled a wider range of occurrence-record datasets to be analysed[25,26]. We explore long-term changes in UK biodiversity through an analysis of the average annual occupancy of invertebrate groups, bryophytes and lichens over a 45-year period. Occupancy is a measure of species range area: in this study (and following others[12,27,28]), occupancy refers to the proportion of 1 km^2 grid cells in which a species is present.

We analyse outputs from national-scale models of annual occupancy spanning 1970–2015 for over 5,000 terrestrial and freshwater species from 31 groups including many insect families, other invertebrate groups, bryophytes and lichens[29]. We quantify trends in average occupancy across taxa and over time and explore differences between common and rare species. We believe that this study represents the most comprehensive assessment of its kind, with unprecedented scale and scope for a national biodiversity assessment.

Results

Multispecies trends in occupancy. Our data are comprised of occupancy estimates for 5,214 species in 31 taxonomic groups for each year from 1970 to 2015[29]. These estimates are derived from hierarchical Bayesian occupancy-detection models for each species and are based on 24,090,792 presence-only biological records. Multispecies trends are summarized for four aggregate taxonomic and habitat-based groups. Freshwater species ($n = 318$) are considered separately from terrestrial species, since they are subject to different pressures. Terrestrial species are aggregated into three groups reflecting major taxonomic boundaries: terrestrial insects ($n = 3{,}089$, hereafter referred to as insects), terrestrial non-insect

---

[1]Centre for Ecology & Hydrology, Wallingford, UK. [2]Centre for Biodiversity and Environment Research, University College London, London, UK. [3]RSPB Centre for Conservation Science, RSPB, Sandy, UK. [4]Department of Statistical Science, University College London, London, UK. [5]Deceased: Ben Collen. *e-mail: charlotte.outhwaite.14@ucl.ac.uk

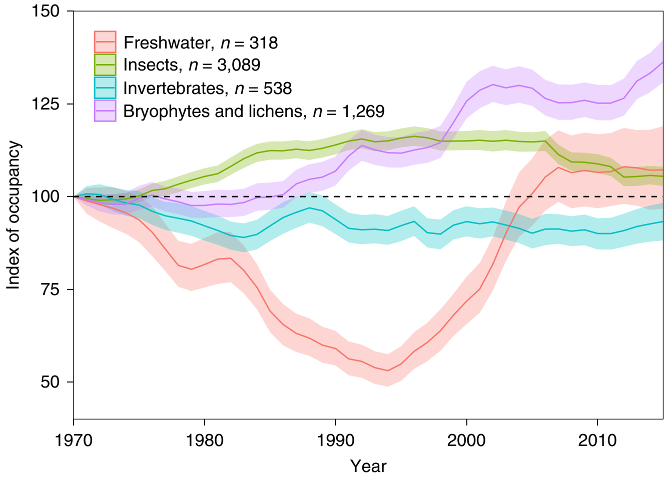


Fig. 1 | Composite estimates of the average annual occupancy of four groups of species. Values are scaled to 100 in 1970. The coloured lines show the average response as the geometric mean occupancy, and the shaded areas represent the 95% credible intervals of the posterior distribution of the geometric mean; *n* denotes the number of species contributing to each group. The uncertainty for each year is expressed relative to the 1970 baseline. The change metrics reported in the text account for the uncertainty in both the first and last years of the series.

invertebrates (mostly spiders, *n* = 538, hereafter invertebrates), and bryophytes and lichens (*n* = 1,269).

Across all 5,214 species, an index of overall occupancy, estimated as the geometric mean occupancy, was 11% higher in 2015 than in 1970 (95% credible interval: 9%, 13%), contradicting the narrative that declines are pervasive. However, there were substantial differences among major groups. The most striking response was seen for the freshwater species. Although this group has experienced little net change since 1970 (+7.2%: −3.3%, +19%), an increase is observed after two decades of consistent decline (Fig. 1). At its lowest point, in 1994, freshwater species occupancy had declined by 47% (−51%, −42%) compared with levels in 1970. Insects show a slight increase in occupancy of 5.5% (+2.9%, +8.1%) and bryophyte and lichen occupancy increased by 36% (+31%, +42%). The invertebrates are the only group to experience an overall decline in mean occupancy with a reduction of 6.7% (−12%, −1.6%).

Temporal variation in the trends is clearly apparent when contrasting the net change in average occupancy during the first (1970–1992) and second (1993–2015) halves of the series (Fig. 2). Freshwater species experienced an extreme change in trajectory, with the fastest declines exhibited across groups experienced before 1992, and the fastest increase across groups after 1992. Insects and invertebrates show opposite patterns with the former presenting an increase pre-1992 and a decline post-1992, and the latter declining initially and then stabilizing. Bryophytes and lichens show a slow increase pre-1992 and then a more rapid increase post-1992. None of the four groups declined consistently across the period assessed: the freshwater and insect groups experienced a reversal in the

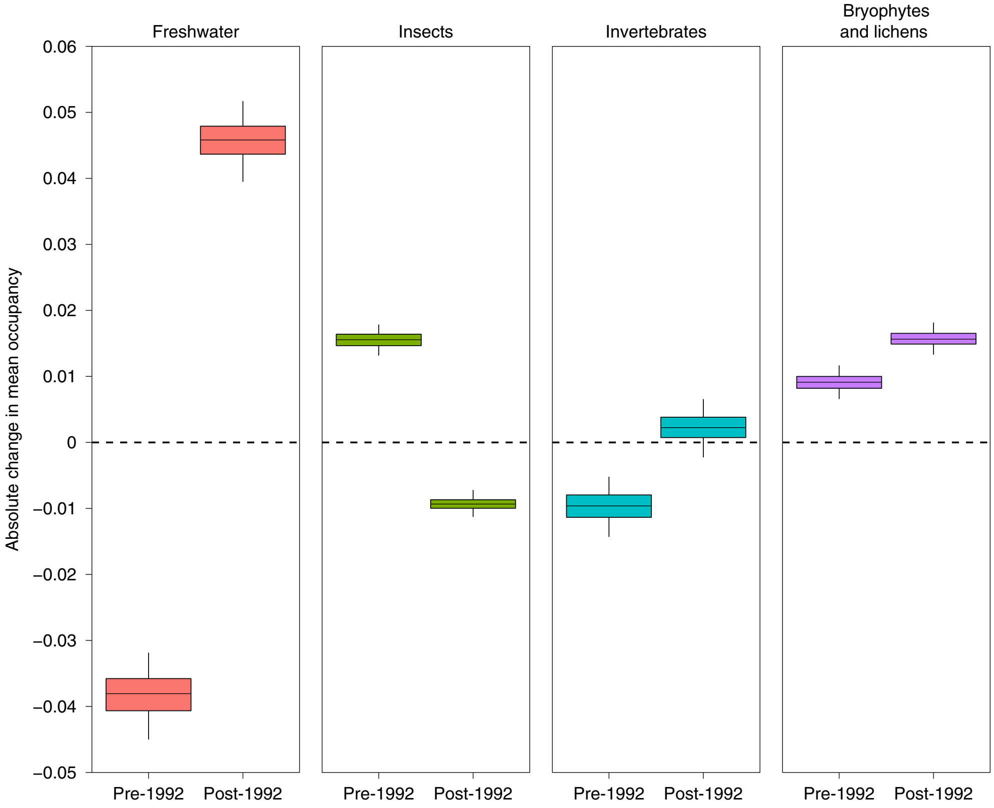


Fig. 2 | Absolute change in geometric mean occupancy during the first (1970–1992) and second (1993–2015) halves of the time series for each major group. Each box plot represents the posterior distribution of the overall absolute change in occupancy within the group, over the relevant time period. The centre of the box plot represents the median of the distribution, and the lower and upper hinges correspond to the 25th and 75th percentiles. The whiskers represent the 95% credible intervals.

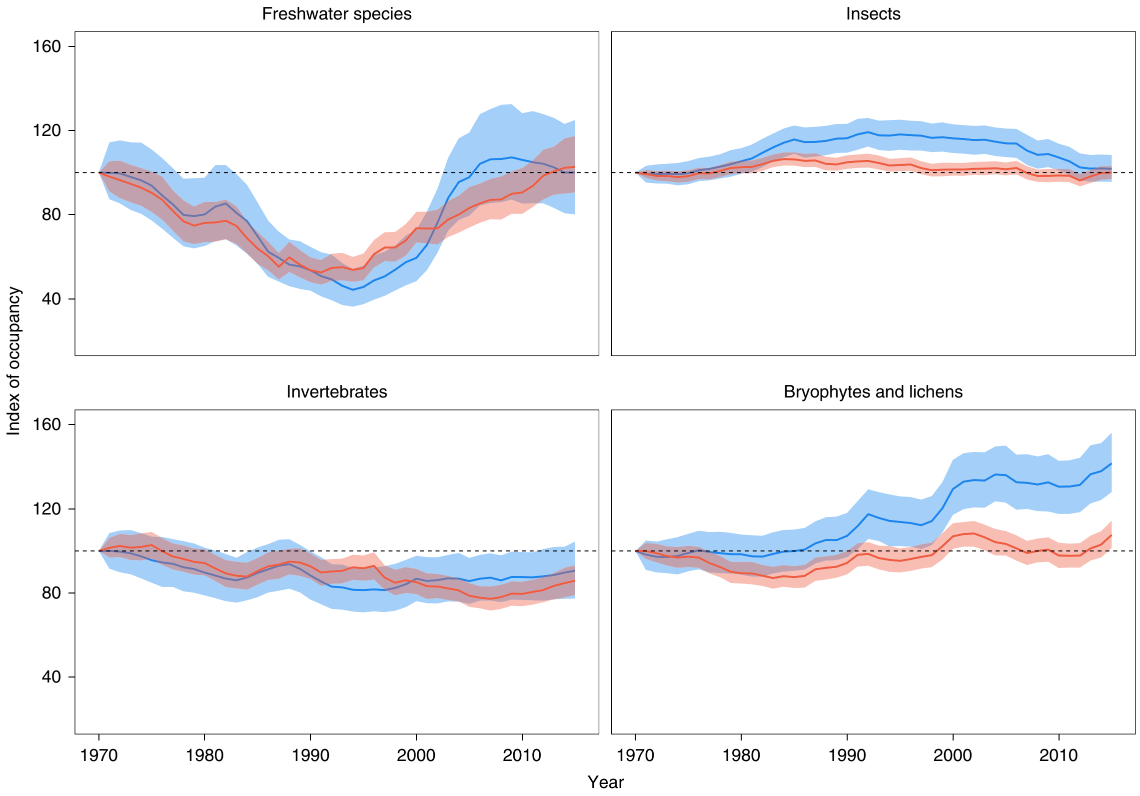


Fig. 3 | Composite estimates of two quantiles of annual occupancy across the four major groups. Two quantiles were chosen to represent varying levels of occupancy: common or widespread (0.75, orange) and rare or localized occupancy (0.25, blue). These quantiles of occupancy were assessed each year to show how rareness and commonness changed over time for each group. In each case, the shaded area delimits the 95% credible interval.

average trend from the early and late parts of the time series. This disparity across groups highlights the potential variability in responses to specific drivers of change and/or responses to a variety of drivers.

We detected variation in the magnitude and timing of changes in the status of rare and common species among groups (Fig. 3). For both the insects and the bryophytes and lichens, the rare species showed greater changes in occurrence than the common species. Conversely, the pattern of change for the common freshwater species indicates an earlier start to the recovery phase than for rare species. Invertebrates present no difference in responses between rare and common species, implying that the composition of invertebrate communities has changed less than in the other groups. The differing responses between rare and common species observed for some groups indicate species turnover in local communities with rare species becoming more common or vice versa.

There is considerable heterogeneity within the four groups, with some taxa facing substantial declines that are not apparent from the average group-level change (Fig. 4); this is particularly evident for the insect group. Most taxa in the freshwater group show the U-shaped trajectory of the average response. The overall decline of the invertebrates is driven mainly by spiders during the early period and by terrestrial molluscs more recently. Bryophytes and lichens increase overall, but the timings of these increases differ. Across all 31 taxonomic groups, 10 increased in mean occupancy (95% credible intervals for the year 2015 do not span 100), and 5 decreased (see Supplementary Table 1 and Supplementary Fig. 1 for more details).

Aggregating species-level change into indicators of average occupancy over time hides the variation among species. Within any group, there will be winners and losers whose responses are more extreme than that of the average[30]. The analysis of the annual growth rates (year-to-year change) in occupancy of individual species reveals that although the mean change in occupancy is an increase of 11%, there are species that have undergone substantial declines (some of which started out relatively common), as well as initially rare species that have increased markedly over time (Fig. 5). There is little correlation between the average occupancy and average growth rate for any of the four major groups (Pearson's correlation coefficient: freshwater, −0.078; insects, 0.002; invertebrates, −0.061; and bryophytes and lichens, −0.0001). Although most species can be found around the zero line, there are large numbers of species whose distributions changed substantially. The lowest decile ($n = 529$) of species' growth rates is −2.1%; that is, 10% (529) of species declined by at least 2.1% each year. Across the full range of 46 years in our dataset, this corresponds to a loss of 62% of previously occupied grid cells. The upper decile is 2.4%; that is, 10% of species increased by at least this amount each year, corresponding to a tripling in distribution over 46 years. Determining the drivers of change and those species most likely to exhibit strong responses will aid in the mitigation of future losses.

Discussion

Our analysis of changes in occupancy for over 5,000 UK species has shown that only one of the four aggregate groups, the invertebrates, presents a decline in average occupancy. On the basis of widely reported declines in the abundance of UK birds[31] and butterflies[3], and of other taxa globally[2,32], one might expect to see declines in occupancy, but our results confound this expectation. Not only is the overall net change positive; the direction of change is different among groups, and there is enormous variation among taxa in the temporal patterns of change and the relative fates of rare and common species. By broadening the taxonomic scope of investigation to these lesser-known groups, our results challenge the received wisdom that all biodiversity change is loss, and that it is both pervasive and unalterable.

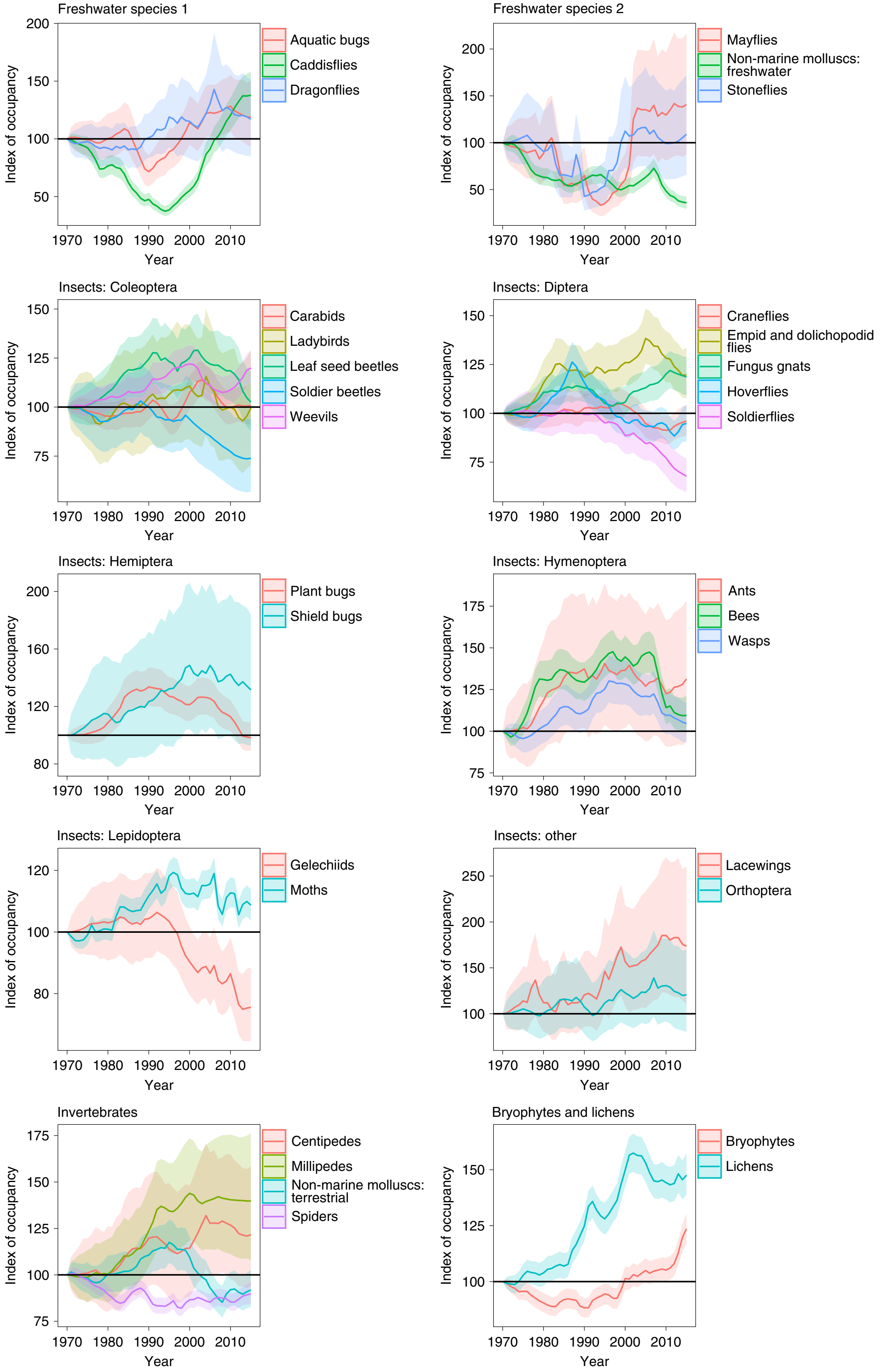


Fig. 4 | Composite estimates of average annual occupancy for each taxonomic subgroup. Taxa in the freshwater and insect groups are displayed across multiple panels to aid visibility. Values are scaled to 100 in 1970. The coloured lines show the average response as the geometric mean occupancy, and the shaded areas represent the 95% credible intervals of the posterior distributions of annual occupancy estimates. The width of each credible interval is a function of the number of species in the group. Note that the *y* axis scales vary.

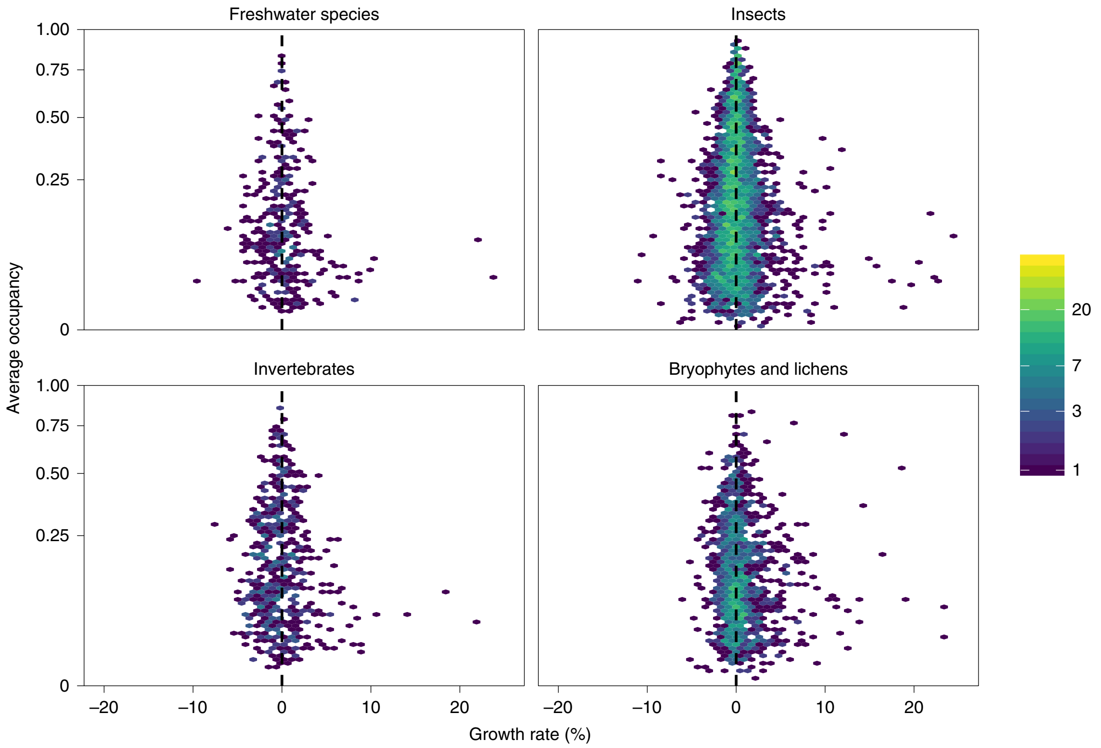


Fig. 5 | Heat map of the comparison between each species' average occupancy estimate across the entire period and its average annual growth rate for each of the four major groups. The colour scale indicates the number of species in each hexagon. The growth rate is expressed as a percentage of the initial occupancy (see Methods). The greater the average occupancy value on the *y* axis, the more common the species. Hexagons to the left of the vertical, dashed line (growth rate, 0) include species with negative annual growth rates; those to the right have positive annual growth rates. Six extreme positive growth rates are not shown.

The increasing trajectories among bryophytes and lichens (since 1970) and the freshwater group (since 1994) suggest a beneficial impact of environmental regulations and consequent management changes in reversing biodiversity declines. Bryophytes and lichens are known to be particularly sensitive to acidic pollutants such as sulfur dioxide[33], and the atmospheric concentrations of these chemicals have been declining since the first Clean Air Act of 1956. Overall, freshwater species experienced substantial declines until the mid-1990s, followed by a recovery to 1970 levels. This U-shaped trajectory is replicated for four of the six freshwater taxa, suggesting a common response to a single driver. It is notable that the lowest mean occupancy for the freshwater group follows shortly after the introduction of the European Urban Wastewater Treatment Directive in 1991 and the step change in the regulation of the water industry after privatization in 1989[34]. Improvements in water quality have been linked to increases in the family-level richness of freshwater invertebrates in Great Britain from the early 1990s onward[35,36] and historically at sampling locations in England[37]. The recent increases we report must be seen in the context of much larger declines that probably occurred over two centuries since the industrial revolution. This makes it hard to interpret the relative trajectories of rare and common species, or the apparent stasis in freshwater occupancy since 2005. Nonetheless, the recoveries in bryophytes, lichens and freshwater species, concomitant with improvements in air and water quality over recent decades, contribute to a growing trend of optimistic narratives in debates about biodiversity conservation[9,38].

Caveats about declines before 1970 also apply to the other major groups under consideration. It is well established that major transformations of the UK landscape occurred during the middle parts of the 20th century[39,40], so care is needed to avoid the pitfalls of shifting baseline syndrome[41,42]. The values from 1970 must not be seen as targets to be reached, since it is likely that levels in 1970 were also considerably lower than earlier in the century.

It should be noted that both recent colonist species and non-native species (such as the Harlequin ladybird) are included in the set of species analysed here, since they also contribute to UK biodiversity change[43]. However, their low numbers (56 species, just over 1% of the total; see Methods for a break-down) result in very little influence on the multispecies trajectories presented here.

Our results demonstrate the insights that can be gathered from careful analysis of presence-only occurrence records. However, they raise questions about how trends in occupancy should be interpreted in the context of more widely used metrics, such as changes in abundance[2], species richness[44], biomass[10,45] or other measures of range size[46,47]. For example, changes in total abundance[48], in total biomass[10] or in average species abundance[3,31] measure similar, but subtly different, facets of biodiversity. Here, our focus is on the average change across species (as in biodiversity indicators), so we assess the average occupancy across species and changes therein. In general, we would expect that trends in average occupancy would underestimate trends in average abundance, but that the two metrics would be closely correlated[49–51]. Indeed, van Strien et al., when assessing trends in both the occupancy and the abundance of butterflies in the Netherlands, observed greater changes in average abundance than in average occupancy, but both metrics presented an overall negative trend[52]. Similarly, species richness and occupancy can be thought of as alternative ways of summarizing a three-dimensional space–time–species data cube in which the cells of the cube represent the binary presence–absence state[53,54]. Typically, if the average occupancy goes up, the average richness per grid cell will also go up, so trends in richness and occupancy should be closely correlated.

This study takes us a step closer to understanding the status of UK biodiversity by exploring patterns of change for groups of species that have previously been neglected in large-scale studies of change. It is clear that occupancy is a valuable tool for assessing patterns over time when abundance data are not available. Over time, the available models and required computation times will improve, enabling the wider application of occupancy modelling with models developed specifically to suit each dataset rather than the one-size-fits-all approach taken to generate the estimates used here. Although more bespoke modelling approaches could deliver greater insights when exploring change for individual species, we believe that this approach is a reasonable trade-off since we are interested in aggregated trends, and this is the only and best information available for most of these species groups. This work presents just one facet in the multifaceted nature of biodiversity change[55].

Methods

The details of the methods used in the analyses presented here are described below. These analyses can be recreated using the original data through the associated R package UKBiodiversity. This R package is available from GitHub (https://github.com/CharlieOuthwaite/UKBiodiversity). The package vignette contains detailed instructions for reproducing each of the statistics and figures presented here.

Data. A species occurrence dataset, as presented by Outhwaite et al.[29], was used to assess annual species occupancies and determine estimates of annual growth rates. This dataset includes 1,000 samples from the posterior distribution of occupancy estimates for 5,293 species from 1970 to 2015. These data are freely available from the Natural Environment Research Council (NERC) Environmental Information Data Centre (https://doi.org/10.5285/0ec7e549-57d4-4e2d-b2d3-2199e1578d84)[29]. An associated Shiny app (https://shiny-apps.ceh.ac.uk/speciesplotviewer/) can be used to view occupancy and detection plots for individual species, although we emphasize that the models developed here may not be optimal for every species considered; the plots should therefore not be used uncritically for single-species assessments. These estimates are derived from occurrence records analysed using a Bayesian occupancy modelling framework based on that of Outhwaite et al.[25]. The model used is a hierarchical model that separates occupancy and detection to allow for the accounting of imperfect detection. Imperfect detection and other biases are common in occurrence record datasets such as those used by Outhwaite et al.[29]; however, occupancy modelling has been shown to be the most appropriate method for analysing this form of data[26]. The model used to generate the occupancy estimates analysed here is made up of the following submodels.

The state model describes the true occupancy state, z_{it}, of a site i in year t (equations (1) and (2)). The value of z_{it} will be 1 when a site is occupied and 0 when it is not occupied. The true occupancy, z_{it}, then takes a Bernoulli distribution:

$$z_{it} \sim \text{Bernoulli}(\psi_{it}) \tag{1}$$

The logit of the probability of occurrence, ψ_{it}, varies with both year, t, and site, i:

$$\text{logit}(\psi_{it}) = \log\left(\frac{\psi_{it}}{1-\psi_{it}}\right) = b_{tr(i)} + u_i \tag{2}$$

The variable $b_{tr(i)}$ is the year effect for year t in region r in which site i is found. The variable u_i is the site effect.

The observation model describes the data collection process. It is conditional on z_{it}. The variable p_{itv} is the probability that a species will be observed on a single visit v, given that the species is present at that site. The observation, y_{itv}, is then drawn from a Bernoulli distribution conditional on z_{it}:

$$y_{itv}|z_{it} \sim \text{Bernoulli}(p_{itv} z_{it}) \tag{3}$$

Variation in detection probabilities, p_{itv}, is described as

$$\begin{aligned} \text{logit}(p_{itv}) = \log\left(\tfrac{p_{itv}}{1-p_{itv}}\right) = a_t + \beta_1 \text{datatype2}_{itv} \\ +\beta_2 \text{datatype3}_{itv} \end{aligned} \tag{4}$$

where β_1 and β_2 estimate differences in logit(p_{itv}) for a list length of two to three (datatype2) and of four or more (datatype 3), respectively, relative to a list length of one, and a_t is a year effect.

The full details of the model used can be found in the data paper associated with the species occurrence dataset[29]. All species included in the species occurrence dataset are used here except the rove beetles (79 species). The rove beetles have data only for 1980 onwards. Since the indicators we present start at 1970, it was decided that this group would be removed to maintain a simple indicator method. We therefore assess changes in occupancy over time for 5,214 species. The dataset contains derived estimates of annual occupancy, with appropriate measures of uncertainty, for species with at least 50 records (see ref. [29] for more detail). Although this is very few records across the 45-year period, increasing this threshold to 200 records per species did not materially change the trajectories of the aggregate group-level changes observed in Fig. 1 (see Extended Data Fig. 1). A higher threshold was therefore deemed unnecessary.

We conducted a posterior predictive checking exercise to assess whether our models are appropriately parameterized and not over- or underfit (see 'Posterior predictive checking'). Since the inferences in the paper are about trends in large multispecies taxa, we calculated summaries for groups of species rather than for individual species.

Species grouping. Species were aggregated into four major groups. Freshwater species were analysed separately, and the terrestrial species were split into three groups (Supplementary Table 2). Freshwater molluscs were separated from terrestrial molluscs on the basis of expert opinion and web-based searches. Each of the 31 taxonomic groups considered here represents a single family (for example, ants, family Formicidae), a selection of families (for example, plant bugs) or a grouping of higher taxonomic rank (for example, caddisflies, order Trichoptera). These groups represent the sets of species recorded by separate recording schemes in the United Kingdom (more information on these schemes can be found at https://www.brc.ac.uk/recording-schemes).

Recent colonists and non-native species have not been excluded from this study. Owing to their small number in each of the four aggregate groups, their influence on the overall patterns of change in this study is minimal (Supplementary Table 3). Most of the species known to be recent colonists to the United Kingdom that are included in this study are moths ($n = 32$). These species were identified from two lists: a list of recent colonists to the United Kingdom established from the literature and a list of established non-native species derived from the GB Non-native Species Secretariat Information Portal species register.

Composite trends. The composite multispecies indicators (as shown in Figs. 1, 3 and 4) are calculated as the geometric mean across species[56]. To generate these indicators, we used the posterior samples of the occupancy estimates for each species in each year provided in the POSTERIOR_SAMPLES folder of the data source[29]. These consist of 1,000 samples describing the proportion of occupied sites per species per year. For each group of species (per taxa or per aggregate group), the 1,000 samples for each species in that group or taxon were assessed. For each group (or taxon), the multispecies structure was represented in the following way:

$$Y_{ist} = \alpha_t + \beta_{st} + \varepsilon_{ist} (t = 1, \dots, T; s = 1, \dots, S; i = 1, \dots n) \tag{5}$$

where T is the total number of years considered, S is the total number of species, n (1,000 here) is the number of posterior samples and Y_{ist} is the logarithm of the ith posterior occupancy sample for species s in year t. In this representation, α_t denotes the posterior index of overall log-occupancy in year t; β_{st} is an adjustment representing the extent to which species s differs from this overall value; and the $\{\varepsilon_{ist}\}$ are independent random variables, each with expectation zero over the posterior distribution, representing the posterior variation for each species–year combination. To ensure that the representation (5) is unique and that α_t has the desired interpretation, the constraint $\sum_{s=1}^{S} \beta_{st} = 0$ is imposed for each year. Without this constraint there are $T + TS$ coefficients (the $\{\alpha_t\}$ and $\{\beta_{st}\}$ in equation (5)), but only TS species–year combinations in the posterior dataset. With T constraints in total on the $\{\beta_{st}\}$, the redundancy is removed.

Define $\bar{Y}_{it} = S^{-1} \sum_{s=1}^{S} Y_{ist}$, the mean of the ith posterior samples across all species at year t. Under the assumption that the posterior occupancy probabilities for different species are independent, the quantities $\{\bar{Y}_{it} : i = 1, \dots, n\}$ are themselves samples from the posterior distribution of overall log-occupancy for year t (the independence assumption is needed to justify combining posterior samples across species). Each has the expected value

$$\mathbb{E}(\bar{Y}_{it}) = S^{-1} \mathbb{E}\left(\sum_{s=1}^{S} Y_{ist}\right) = S^{-1} \mathbb{E}\left[\sum_{s=1}^{S} (\alpha_t + \beta_{st} + \varepsilon_{ist})\right] = \alpha_t \tag{6}$$

The remaining terms vanish because $\sum_{s=1}^{S} \beta_{st} = \mathbb{E}(\varepsilon_{ist}) = 0$. Therefore, if n is large, then the mean of the $\{\bar{Y}_{it} : i = 1, \dots, n\}$ will be close to α_t, the desired index of overall log-occupancy. Thus, $e^{\bar{Y}_{it}}$ corresponds to the geometric mean occupancy, which we present in Figs. 1 and 4, after rescaling to start at 100 in 1970, with the mean and 95% quantiles taken to summarize the uncertainty of this index. To determine whether the patterns observed in Fig. 1 were due to specific species responses within these groups rather than random variation, the indicators were all recalculated for alternative datasets produced by randomly reassigning species to major groups in such a way that each group contained the same number of species as in reality. This reassignment, which is carried out in the spirit of a permutation test (ref. [57], Section 3.3), ensures that any intergroup differences in the alternative datasets can be due only to random variation. Our results, such as those in Extended Data Fig. 2, do not show the kinds of patterns that are observed in Fig. 1; these patterns therefore represent genuine intergroup differences rather than random interspecies variation.

The indices presenting changes in rarity and commonness of species over time (Fig. 3) were calculated in a similar way. Specifically, rather than estimating the geometric mean occupancy $\{\bar{Y}_{it}\}$ across species posterior samples within a major group, we estimated the quantiles $\{Q_{it}\}$ corresponding to rare species (25th percentile) and common species (75th percentile). Figure 3 then summarizes the posterior distributions $\{100e^{Q_{it}-Q_{i1}}\}$ for each of these quantiles.

The percentage change in occupancy of all species and aggregate groups, presented in the main text, was calculated using the geometric mean occupancies for the first, $\bar{Y}_{i1}$, and last years, $\bar{Y}_{iT}$ (1970 and 2015, respectively):

$$\delta_i = 100\left(e^{\bar{Y}_{iT}} - e^{\bar{Y}_{i1}}\right)/e^{\bar{Y}_{i1}} \tag{7}$$

Similarly, annual growth rates, λ_i, for each species, provided in the data source, were calculated as:

$$\lambda_{is} = 100\left(\left(\frac{Y_{isT}}{Y_{is1}}\right)^{\frac{1}{T}} - 1\right) \tag{8}$$

For the calculation of species' growth rates, we used only the first ($t=1$) and last ($t=T$) years in which the species was recorded, to avoid any bias due to the potential information in the priors[25].

Sensitivity of the indicators to the number of records of a species. The dataset of annual occupancy estimates for UK species that formed the basis of this analysis included modelled outputs for species that had 50 records or more in the raw dataset (see ref. [58] for more details). This is a very low number of records across the dataset that encompasses the years 1970 to 2015. To ensure that species with few records were not having a large influence on the overall trends and patterns of change over time, we recalculated the major group indicators presented in Fig. 1 of the main text but used higher thresholds for the number of records of a species (Extended Data Fig. 1). Overall, higher thresholds (including 75, 100, 150 and 200 records minimum per species) did not have a major effect on the patterns of change over time observed in Fig. 1. Trends differed slightly, such as for bryophytes and lichens in some instances, but no major differences or changes in direction were seen.

Variability within major group-level indicators. Considering that the major group indicators present the average change across hundreds to thousands of species, it is likely that the variation across species will be high. To determine whether the observed patterns resulted from this random variation or represented common responses across species, we recreated the indicators presented in Fig. 1 but randomized the species in each major group. So, for each of the four major groups, the same total number of species in it was maintained, but the species identified were randomly selected from the complete species pool. This species randomization and indicator generation were carried out 12 times to see whether the observed patterns of change could be recreated from the randomly selected set of species. Extended Data Fig. 2 shows the analogue of Fig. 1 for each of the 12 alternative datasets obtained by randomization in this way. For most of them, all four groups show very similar trends in occupancy that are similar to the overall increase of 11% reported in the main text; the fifth alternative dataset shows a separation into two pairs of groups. None of these alternative datasets, however, shows structures similar to those presented in Fig. 1. This provides reassurance that those structures are indeed associated with genuine intergroup differences and cannot be attributed merely to random interspecies variation.

Posterior predictive checking. This section presents the results of some diagnostics that have been used to check our models' ability to reproduce selected features of the observations as aggregated over species groups. These checks have been carried out to provide some reassurance that the models are sufficiently flexible and realistic to capture the structures seen in the data, and hence to support the use of the models to make statements about long-term changes in occupancy.

Posterior predictive checking is a Bayesian technique that is designed to assess how well a model reproduces features of a dataset[59]. The basic principle is, having fitted a model to a set of observations, y, to generate from the model a corresponding data vector, y_{rep}. If the data are appropriately parameterized, then y and y_{rep} should be similar.

In the case of an occupancy-detection model, the observations for each species' model constitute a vector containing an entry of 0 or 1 for each relevant visit in the database—1 if the species was reported, 0 otherwise. Similarity is defined by comparing relevant properties of the observed and simulated data vectors.

In our models, the values of y, the observed detections, are assumed to be generated probabilistically, and therefore the observed summary $T(y)$ is also drawn from some probability distribution. Formally, it's the realized value of a random variable $T(Y)$, where Y is a random vector whose joint distribution is specified by the model. We don't know exactly what this distribution is because, even if the model structure is correct, we don't know the parameter values exactly. However, we do have a posterior distribution for the parameters. If we draw repeated samples from this posterior distribution and, for each sample, use the model to generate a synthetic data set, y_{rep}, and calculate the corresponding summary $T(y_{\text{rep}})$, then we can build up a collection of samples from a distribution of $T(\cdot)$ that accounts both for the randomness in the model and for the parameter uncertainty. Such a distribution is called a posterior predictive distribution. The observed summary $T(y)$ can then be compared with the posterior predictive distribution as a check on model performance.

In the present context, for each species the replications y_{rep} need to be generated to mimic as closely as possible the process that generated the data under the model: the same sites, numbers of visits and associated list lengths. Two separate summary measures $T(y)$ were calculated for each group of species. The first was the overall proportion of sites with a detection, averaged over all species and years; the second was the variance in the annual mean proportion of detections for the group (see below). This choice enables us to check the model's ability to reproduce features at the same level of group aggregation as the main analyses in the paper; moreover, the variance in annual mean detections is a measure of interannual variation, which is related to the indices of change in the paper. Of course, it is not possible to compare the modelled occupancies with the observations, because occupancy is not observed; since detection is conditional on occupancy, however, we may have some confidence that models represent the properties of the aggregated occupancies reasonably well if they can represent the corresponding properties of the aggregated detections. We implemented the following protocol for each taxonomic group:

(1) For each of v visits in each species' model, extract 99 samples from the posterior distribution of the probability that an observation was made on that visit. In practical terms, this probability is the product of the true (unknown) occupancy, z_{it}, and the detection probability, p_{itv} (see equation 4 in ref. [58]).
(2) Use each of the 99 sets of probabilities to sample a vector of potential observations under the model, by treating each visit as a potential Bernoulli trial. These vectors are 99 realizations of y_{rep}.
(3) For each realization y_{rep} and for each year (1970–2015), calculate the annual proportion of sites in which the species was recorded; denote this proportion, for species s and year t, by $T_{st}(y_{\text{rep}})$.
(4) Calculate $T_{gt}(y_{\text{rep}})$ for each replicate dataset as the mean of $T_{st}(y_{\text{rep}})$ across species in each taxonomic group, g.
(5) Calculate the mean m across years as $T_{gm}(y_{\text{rep}})$ for each replicate dataset.
(6) Calculate $T_{gvar}(y_{\text{rep}})$ as the variance across years in $T_{gt}(y_{\text{rep}})$ for each replicate dataset.
(7) Calculate the observed mean proportion of sites with records, $T_{gm}(y)$, and the variance across years, $T_{gvar}(y)$, for each replicate dataset.
(8) Summarize the distributions of $T_{gm}(y)$ and $T_{gvar}(y)$ as the mean and 95% credible intervals to demonstrate the variation in summary measures that can reasonably be expected under the model.

Computational limitations made this exercise unfeasible for four groups (bryophytes, dragonflies, moths and lichens). Molluscs are treated as a single group for this exercise since the models were run as a complete group, but the species were split into freshwater and terrestrial for the main analysis.

The mean proportion of sites with records is very well predicted on average, although rather uncertain in many taxonomic groups (Extended Data Fig. 3).

The interannual variability is estimated very precisely by the model for most species (the posterior predictive intervals are narrow; see Extended Data Fig. 4), and shows excellent agreement with the observations for almost all taxonomic groups. There are a few taxa for which the observed value does not fall within the range of the posterior predictive interval, although in absolute terms the discrepancies are sufficiently small as not to compromise the main messages in the paper. The explanation for these discrepancies is either that the model is slightly biased for these species, or that the predictive uncertainties have been underestimated so that the intervals are slightly too narrow.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The dataset analysed as a part of this study is publicly available from the Environmental Information Data Centre[30]. Additional information is supplied in the associated R package UKBiodiversity, which is available from GitHub (https://github.com/CharlieOuthwaite/UKBiodiversity), and Data Descriptor[29].

Code availability

The code used to analyse the data is available from GitHub in the R package UKBiodiversity (https://github.com/CharlieOuthwaite/UKBiodiversity).

Received: 31 July 2019; Accepted: 14 January 2020;
Published online: 17 February 2020

References

1. Gregory, R. D. et al. Developing indicators for European birds. *Phil. Trans. R. Soc. B* **360**, 269–288 (2005).
2. McRae, L., Deinet, S. & Freeman, R. The diversity-weighted living planet index: controlling for taxonomic bias in a global biodiversity indicator. *PLoS ONE* **12**, e0169156 (2017).
3. Brereton, T., Roy, D. B., Middlebrook, I., Botham, M. & Warren, M. The development of butterfly indicators in the United Kingdom and assessments in 2010. *J. Insect Conserv.* **15**, 139–151 (2010).
4. Van Swaay, C. A. M. et al. *The EU Butterfly Indicator for Grassland species: 1990-2017: Technical Report* (Butterfly Conservation Europe & ABLE/eBMS, 2015).

5. Tittensor, D. P. et al. A mid-term analysis of progress toward international biodiversity targets. *Science* **346**, 241–244 (2014).
6. Westgate, M. J., Barton, P. S., Lane, P. W. & Lindenmayer, D. B. Global meta-analysis reveals low consistency of biodiversity congruence relationships. *Nat. Commun.* **5**, 3899 (2014).
7. Rodrigues, A. S. L. & Brooks, T. M. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annu. Rev. Ecol. Evol. Syst.* **38**, 713–737 (2007).
8. Hambler, C. & Speight, M. R. Extinction rates and butterflies. *Science* **305**, 1563–1565 (2004).
9. van Strien, A. J. et al. Modest recovery of biodiversity in a western European country: the living planet index for the Netherlands. *Biol. Conserv.* **200**, 44–50 (2016).
10. Hallmann, C. A. et al. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* **12**, e0185809 (2017).
11. Sánchez-Bayo, F. & Wyckhuys, K. A. G. Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv.* **232**, 8–27 (2019).
12. Powney, G. D. et al. Widespread losses of pollinating insects in Britain. *Nat. Commun.* **10**, 1018 (2019).
13. Simmons, B. I. et al. Worldwide insect declines: an important message, but interpret with caution. *Ecol. Evol.* **9**, 3678–3680 (2019).
14. Thomas, C. D. & Jones, T. H. & Hartley, S. E. 'Insectageddon': a call for more robust data and rigorous analyses. *Glob. Change Biol.* **25**, 1891–1892 (2019).
15. Burns, F. et al. Agricultural management and climatic change are the major drivers of biodiversity change in the UK. *PLoS ONE* **11**, e0151595 (2016).
16. Burns, F. et al. An assessment of the state of nature in the United Kingdom: a review of findings, methods and impact. *Ecol. Indic.* **94**, 226–236 (2018).
17. Hayhow, D. et al. *The State of the UK's Birds 2017* (RSPB, BTO, WWT, DAERA, JNCC, NE and NRW, 2017).
18. Fox, R. et al. *The State of the UK's Butterflies 2015* (Butterfly Conservation and the Centre for Ecology & Hydrology, 2015).
19. Maskell, L. C., Smart, S. M., Bullock, J. M., Thompson, K. & Stevens, C. J. Nitrogen deposition causes widespread loss of species richness in British habitats. *Glob. Change Biol.* **16**, 671–679 (2010).
20. Barlow, K. E. et al. Citizen science reveals trends in bat populations: the National Bat Monitoring Programme in Great Britain. *Biol. Conserv.* **182**, 14–26 (2015).
21. Pocock, M. J. O., Roy, H. E., Preston, C. D. & Roy, D. B. The Biological Records Centre: a pioneer of citizen science. *Biol. J. Linn. Soc.* **115**, 475–493 (2015).
22. Isaac, N. J. B. & Pocock, M. J. O. Bias and information in biological records. *Biol. J. Linn. Soc.* **115**, 522–531 (2015).
23. Boakes, E. H. et al. Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biol.* **8**, e1000385 (2010).
24. Maldonado, C. et al. Estimating species diversity and distribution in the era of Big Data: to what extent can we trust public databases? *Glob. Ecol. Biogeogr.* **24**, 973–984 (2015).
25. Outhwaite, C. L. et al. Prior specification in Bayesian occupancy modelling improves analysis of species occurrence data. *Ecol. Indic.* **93**, 333–343 (2018).
26. Isaac, N. J. B., van Strien, A. J., August, T. A., de Zeeuw, M. P. & Roy, D. B. Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods Ecol. Evol.* **5**, 1052–1060 (2014).
27. van Strien, A. J., van Swaay, C. A. M. & Termaat, T. Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *J. Appl. Ecol.* **50**, 1450–1458 (2013).
28. Termaat, T. et al. Distribution trends of European dragonflies under climate change. *Divers. Distrib.* **25**, 936–950 (2019).
29. Outhwaite, C. L. et al. *Annual Estimates of Occupancy for Bryophytes, Lichens and Invertebrates in the UK (1970–2015)* (NERC Environmental Information Data Centre, 2019); https://doi.org/10.5285/0ec7e549-57d4-4e2d-b2d3-2199e1578d84
30. Dornelas, M. et al. A balance of winners and losers in the Anthropocene. *Ecol. Lett.* **22**, 847–854 (2019).
31. Gregory, R. & van Strien, A. Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithol. Sci.* **9**, 3–22 (2010).
32. Newbold, T. et al. Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50 (2015).
33. Pescott, O. L. et al. Air pollution and its effects on lichens, bryophytes, and lichen-feeding Lepidoptera: review and evidence from biological records. *Biol. J. Linn. Soc.* **115**, 611–635 (2015).
34. Saal, D. S. & Parker, D. The impact of privatization and regulation on the water and sewerage industry in England and Wales: a translog cost function model. *Manage. Decis. Econ.* **21**, 253–268 (2000).
35. Vaughan, I. P. & Ormerod, S. J. Large-scale, long-term trends in British river macroinvertebrates. *Glob. Change Biol.* **18**, 2184–2194 (2012).
36. Vaughan, I. P. & Gotelli, N. J. Water quality improvements offset the climatic debt for stream macroinvertebrates over twenty years. *Nat. Commun.* **10**, 1956 (2019).
37. Langford, T. E. L., Shaw, P. J., Ferguson, A. J. D. & Howard, S. R. Long-term recovery of macroinvertebrate biota in grossly polluted streams: re-colonisation as a constraint to ecological quality. *Ecol. Indic.* **9**, 1064–1077 (2009).
38. Balmford, A. & Knowlton, N. Why Earth Optimism? *Science* **356**, 225 (2017).
39. Antrop, M. Why landscapes of the past are important for the future. *Landsc. Urban Plan.* **70**, 21–34 (2005).
40. Robinson, R. A. & Sutherland, W. J. Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* **39**, 157–176 (2002).
41. Mihoub, J. B. et al. Setting temporal baselines for biodiversity: the limits of available monitoring data for capturing the full impact of anthropogenic pressures. *Sci. Rep.* **7**, 41591 (2017).
42. Soga, M. & Gaston, K. J. Shifting baseline syndrome: causes, consequences, and implications. *Front. Ecol. Environ.* **16**, 222–230 (2018).
43. Thomas, C. D. *Inheritors of the Earth: How Nature Is Thriving in an Age of Extinction* (Hachette UK, 2017).
44. Dornelas, M. et al. Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**, 296–299 (2014).
45. Lister, B. C. & Garcia, A. Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc. Natl Acad. Sci. USA* **115**, 201722477 (2018).
46. Mace, G. M., Collen, B., Fuller, R. A. & Boakes, E. H. Population and geographic range dynamics: implications for conservation planning. *Phil. Trans. R. Soc. B* **365**, 3743–3751 (2010).
47. Gaston, K. J. & Fuller, R. A. The sizes of species' geographic ranges. *J. Appl. Ecol.* **46**, 1–9 (2009).
48. Seibold, S. et al. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671–674 (2019).
49. Bart, J. & Klosiewski, S. P. Use of presence-absence to measure changes in avian density. *J. Wildl. Manage.* **53**, 847–852 (1989).
50. Webb, T. J., Freckleton, R. P. & Gaston, K. J. Characterizing abundance–occupancy relationships: there is no artefact. *Glob. Ecol. Biogeogr.* **21**, 952–957 (2012).
51. Buckley, H. L. & Freckleton, R. P. Understanding the role of species dynamics in abundance–occupancy relationships. *J. Ecol.* **98**, 645–658 (2010).
52. van Strien, A. J., van Swaay, C. A. M., van Strien-van Liempt, W. T. F. H., Poot, M. J. M. & WallisDeVries, M. F. Over a century of data reveal more than 80% decline in butterflies in the Netherlands. *Biol. Conserv.* **234**, 116–122 (2019).
53. Jetz, W. et al. Essential biodiversity variables for mapping and monitoring species populations. *Nat. Ecol. Evol.* **3**, 539–551 (2019).
54. Schmeller, D. S. et al. An operational definition of essential biodiversity variables. *Biodivers. Conserv.* **26**, 2967–2972 (2017).
55. McGill, B. J. & Dornelas, M. & Gotelli, N. J. & Magurran, A. E. Fifteen forms of biodiversity trend in the Anthropocene. *Trends Ecol. Evol.* **30**, 104–113 (2014).
56. Buckland, S. T., Magurran, A. E., Green, R. E. & Fewster, R. M. Monitoring change in biodiversity through composite indices. *Phil. Trans. R. Soc. B* **360**, 243–254 (2005).
57. Faraway, J. J. *Linear Models with R* (Chapman & Hall, CRC, 2009).
58. Outhwaite, C. L. et al. Annual estimates of occupancy for bryophytes, lichens and invertebrates in the UK, 1970–2015. *Sci. Data* **6**, 259 (2019).
59. Gelman, A. et al. *Bayesian Data Analysis* (CRC, 2014).

Acknowledgements

We thank the following recording schemes and societies for contributing data to the dataset underlying this study and for their input in interpreting group-level change: the Aquatic Heteroptera Recording Scheme; the Bees, Wasps and Ants Recording Society; the British Arachnological Society, Spider Recording Scheme; the British Bryological Society; the British Dragonfly Society: Dragonfly Recording Network; the British Lichen Society; the British Myriapod and Isopod Group: Centipede Recording Scheme; the British Myriapod and Isopod Group: Millipede Recording Scheme; the Chrysomelidae Recording Scheme; the Conchological Society of Great Britain and Ireland; the Dipterists Forum: Cranefly Recording Scheme; the Dipterists Forum: Empididae, Hybotidae and Dolichopodidae Recording Scheme; the Dipterists Forum: Fungus Gnat Recording Scheme; the Dipterists Forum: Hoverfly Recording Scheme; the Gelechiid Recording Scheme; the Grasshoppers and Related Insects Recording Scheme; the Ground Beetle Recording Scheme; the Lacewings and Allies Recording Scheme; the National Moth Recording Scheme; the Riverfly Recording Schemes: Ephemeroptera; the Riverfly Recording Schemes: Plecoptera; the Riverfly Recording Schemes: Trichoptera; the Soldier Beetles, Jewel Beetles and Glow-worms Recording Scheme; the Soldierflies and Allies Recording Scheme; the Staphylinidae Recording Scheme; the Terrestrial Heteroptera Recording Scheme—Plant bugs and allied species; the Terrestrial Heteroptera Recording Scheme—Shield bugs and allied species; the UK Ladybird Survey; and the Weevil and Bark Beetle Recording Scheme. We thank G. Mace, whose advice and comments on previous versions of this manuscript greatly improved the study. We thank T. August, G. Powney, J. Silvertown and R. Pearson for advice and comments on the draft manuscripts. We also thank J. Cranston for supplying a list of recent colonist species in the United Kingdom. This work was funded by NERC, award number NE/L008823/1, and was supported by NERC, award number NE/R016429/1, as part of the UK-SCAPE programme delivering National Capability.

Author contributions

N.J.B.I., B.C. and R.D.G. conceived the study. C.L.O. extracted and analysed the data and drafted the manuscript. R.E.C. determined the composite indicator method. All authors contributed to the writing and editing of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

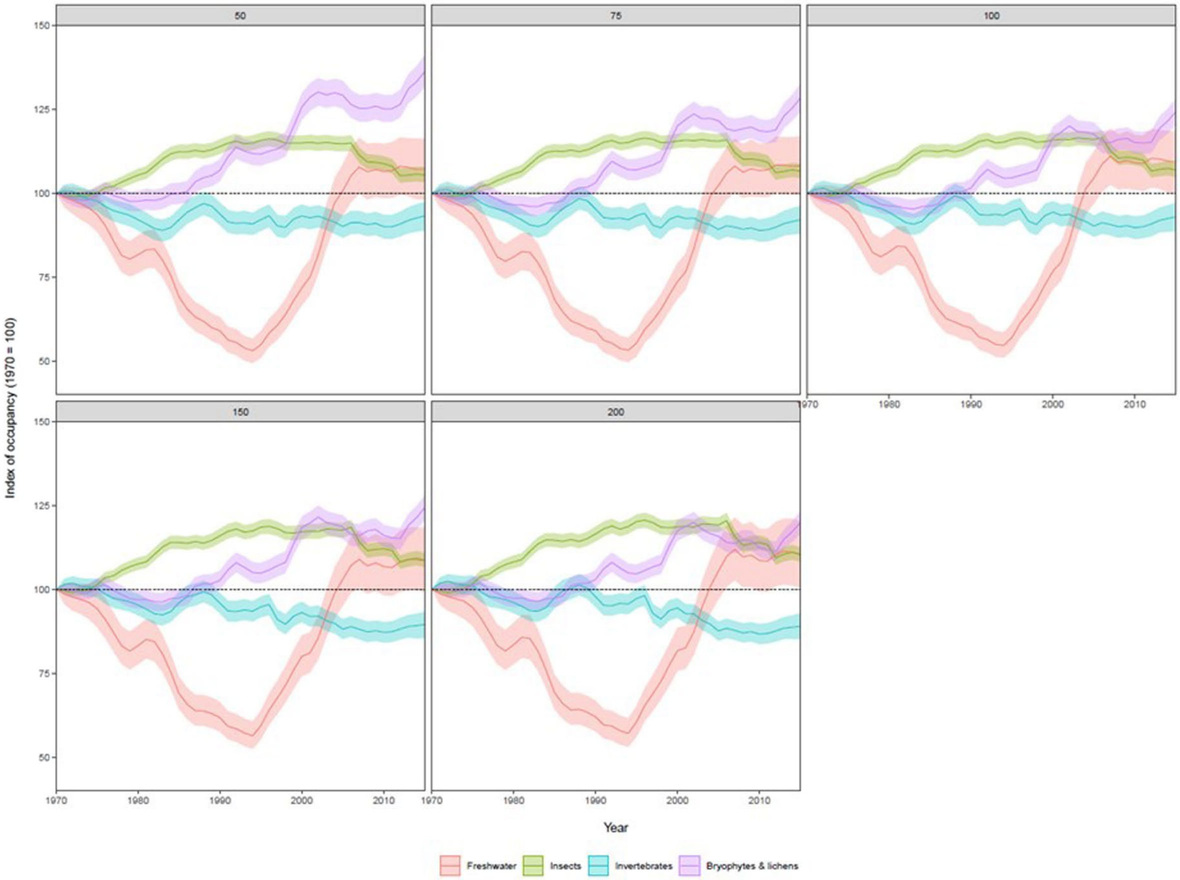
Extended data is available for this paper at https://doi.org/10.1038/s41559-020-1111-z.

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-020-1111-z.

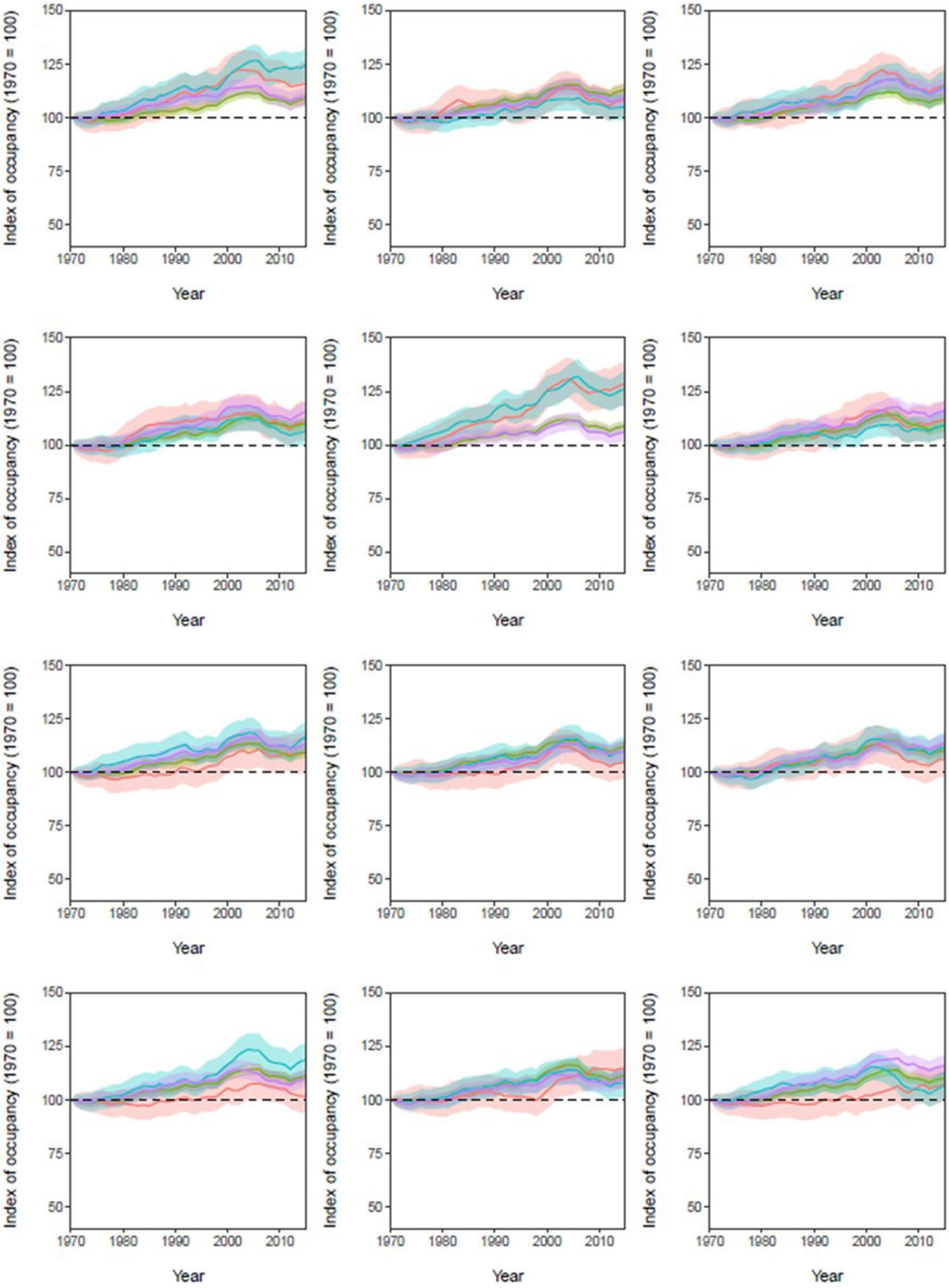
Correspondence and requests for materials should be addressed to C.L.O.

Reprints and permissions information is available at www.nature.com/reprints.

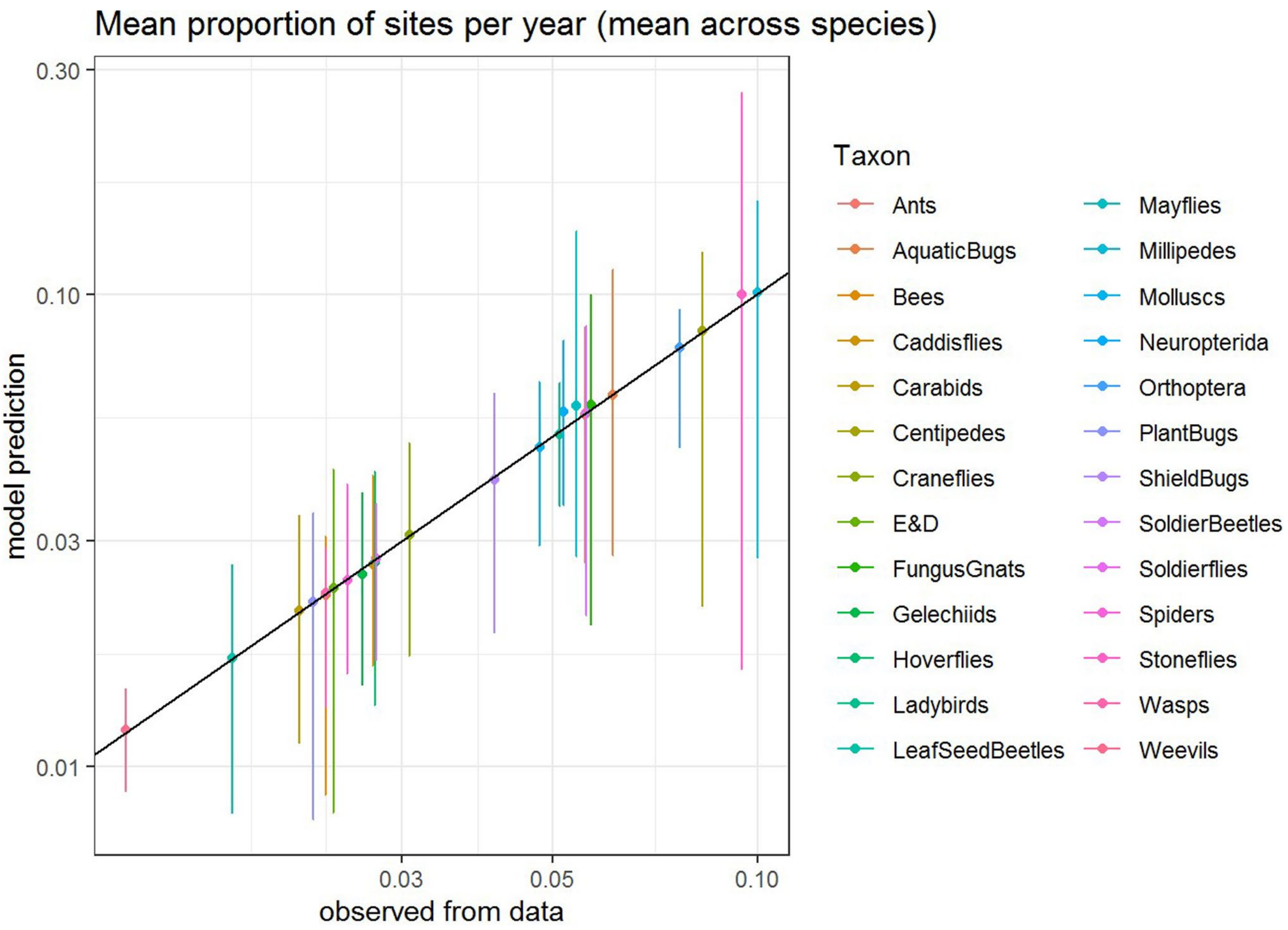
Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



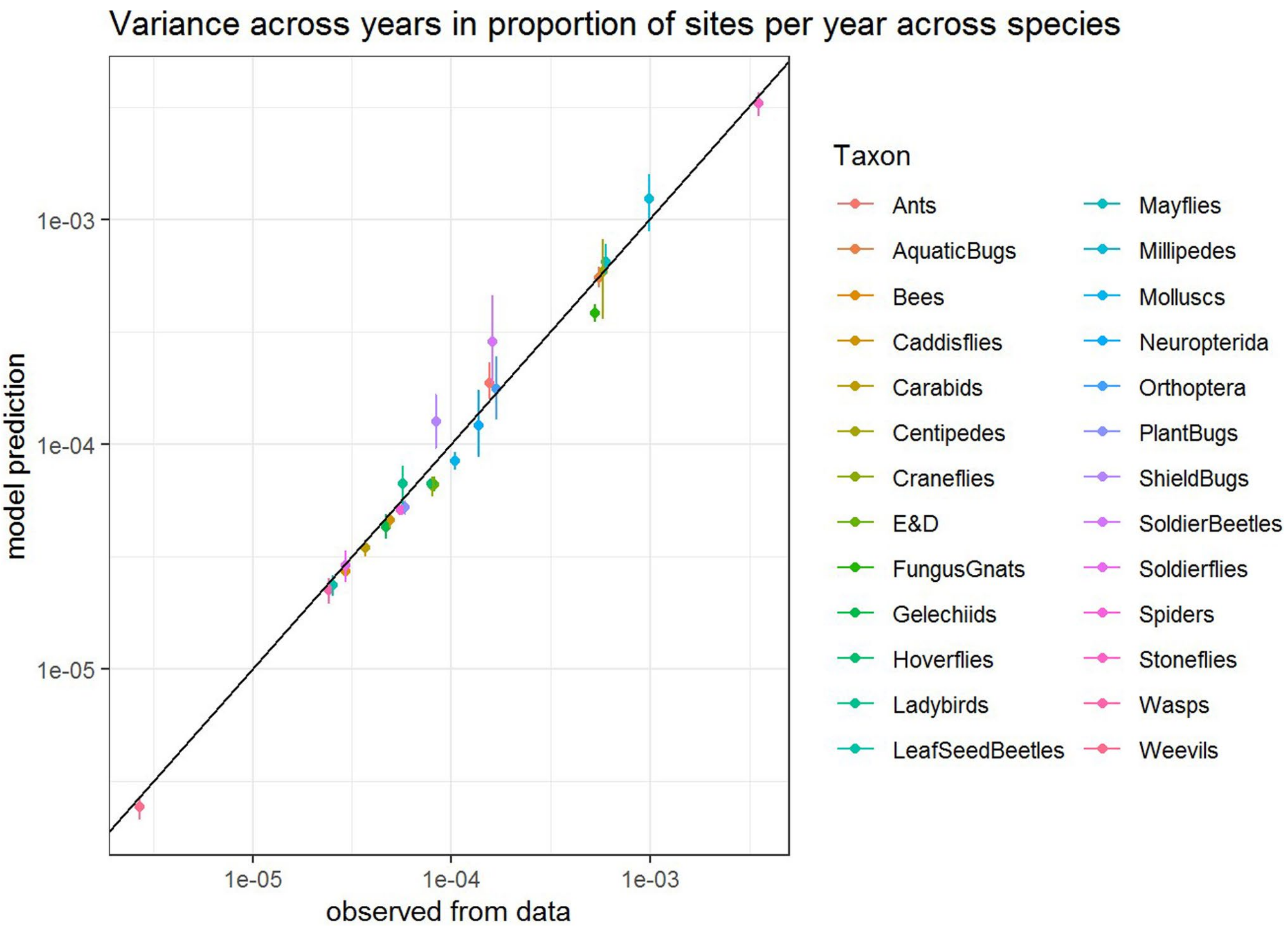
Extended Data Fig. 1 | Figure 1 of the main text, repeated using different thresholds for the number of records that contribute to a species' estimate. Five thresholds were tested: a minimum of 50 records, 75, 100, 150 and 200 records. Each facet presents composite trends in average occupancy of four groups of species. Values are scaled to 100 in 1970. Coloured lines show the average response as the geometric mean occupancy and the shaded area represents the 95% credible intervals of the posterior distribution of the geometric mean.



Extended Data Fig. 2 | Figure 1 of the main text, repeated 12 times whist randomising the species within each group. The colours and number of species within each group are maintained as in Fig. 1 of the main text, however the species have been randomly reassigned across the groups. Red = freshwater (n = 318), green = insects (n = 3089), blue = invertebrates (n = 536) and purple = bryophytes & lichens (n = 1269). Values are scaled to 100 in 1970. Coloured lines show the average response as the geometric mean occupancy and the shaded area represents the 95% credible intervals of the posterior distribution of the geometric mean.



Extended Data Fig. 3 | Mean across years of the species' mean proportion of sites with records for each of 26 taxonomic groups. The black line shows the 1:1 relationship, error bars delimit the 95% credible intervals.



Extended Data Fig. 4 | Variance across years in the species' mean proportion of sites with records for each of 26 taxonomic groups. The black line shows the 1:1 relationship, error bars delimit the 95% credible intervals.

nature research

Corresponding author(s): Charlotte L. Outhwaite

Last updated by author(s): Jan 8, 2020

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
☒	☐	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	The dataset used in this study was directly downloaded from the EIDC repository (https://doi.org/10.5285/0ec7e549-57d4-4e2d-b2d3-2199e1578d84). No software was used to do this.
Data analysis	All data analyses were carried out using R version 3.6. All code is available from GitHub (https://github.com/CharlieOuthwaite/UKBiodiversity).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The dataset analysed as a part of this study is publicly available from the EIDC (https://doi.org/10.5285/0ec7e549-57d4-4e2d-b2d3-2199e1578d84). Additional information is supplied within the associated R package UKBiodiversity which is available from GitHub (https://github.com/CharlieOuthwaite/UKBiodiversity).

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study investigates trends in the average occupancy of over 5000 species of invertebrates, bryophytes and lichens in the UK for the period 1970 to 2015. Indicators of change over time and estimates of trends are derived from outputs of a Bayesian occupancy model study that are publicly available from the EIDC.
Research sample	This study covers over 5000 species of invertebrate, bryophytes and lichens that are found within the UK. This sample encompasses all those species for which estimates of annual occupancy were available from 1970 to 2015 through the associated EIDC repository.
Sampling strategy	All species for which data were available from 1970 to 2015 were used in this study. This species coverage includes all species within the taxonomic group for which annual estimates of occupancy are currently available.
Data collection	The data are derived from a Bayesian occupancy model analysis carried out by Outhwaite et al (2019), details of this can be found in the associated repository documentation and the associated data paper (DOI: 10.1038/s41597-019-0269-1).
Timing and spatial scale	Annual estimates for GB or UK are used for the time period 1970 to 2015.
Data exclusions	From the original dataset, only Rove Beetles were excluded as their data did not cover the complete time period required.
Reproducibility	All analyses and figures can be reproduced using the R package UKBiodiversity which is available through GitHub (https://github.com/CharlieOuthwaite/UKBiodiversity)
Randomization	Randomization was not relevant to this study since data were modeled outputs at a national scale.
Blinding	Blinding was not relevant for this study since data were modeled outputs.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging