

Current Biology

Patterns of invertebrate functional diversity highlight the vulnerability of ecosystem services over a 45-year period

Highlights

- Caddisflies showed a decline and recovery in functional diversity
- Pollinator taxonomic diversity and functional diversity showed opposite patterns
- Pest control agents and pests showed greater stability in functional diversity

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In brief

Greenop et al. show patterns ranging from collapse and recovery to stable trends in functional diversity for invertebrate species supporting key ecosystem services across Great Britain over a 45-year period. These results highlight variability in the long-term vulnerability of key ecosystem services with ongoing biodiversity change.



Report

Patterns of invertebrate functional diversity highlight the vulnerability of ecosystem services over a 45-year period

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SUMMARY

Declines in invertebrate biodiversity^{1,2} pose a significant threat to key ecosystem services.^{3–5} Current analyses of biodiversity often focus on taxonomic diversity (e.g., species richness),^{6,7} which does not account for the functional role of a species. Functional diversity of species' morphological or behavioral traits is likely more relevant to ecosystem service delivery than taxonomic diversity, as functional diversity has been found to be a key driver of a number of ecosystem services including decomposition and pollination.^{8–12} At present, we lack a good understanding of long-term and large-scale changes in functional diversity, which limits our capacity to determine the vulnerability of key ecosystem services with ongoing biodiversity change. Here we derive trends in functional diversity and taxonomic diversity over a 45-year period across Great Britain for species supporting freshwater aquatic functions, pollination, natural pest control, and agricultural pests (a disservice). Species supporting aquatic functions showed a synchronous collapse and recovery in functional and taxonomic diversity. In contrast, pollinators showed an increase in taxonomic diversity, but a decline and recovery in functional diversity. Pest control agents and pests showed greater stability in functional diversity over the assessment period. We also found that functional diversity could appear stable or show patterns of recovery, despite ongoing changes in the composition of traits among species. Our results suggest that invertebrate assemblages can show considerable variability in their functional structure over time at a national scale, which provides an important step in determining the long-term vulnerability of key ecosystem services with ongoing biodiversity change.

RESULTS

Despite the foundational importance of functional diversity in understanding ecosystem service provision,^{9,10,12} we currently lack long-term and large-scale trends. Assessments of biodiversity change have predominantly focused on trends in taxonomic diversity, which quantify changes based on the presence/absence or abundance of different species.^{1,2,6,13} However, species are not necessarily interchangeable in the role they perform in an ecosystem and therefore how they contribute to key ecosystem services, such as pest control, pollination and aquatic nutrient processing, and energy flows.^{5,14,15} Species possess unique morphological or behavioral characteristics, referred to as “effects traits,” that have been shown to directly alter their capacity to contribute to ecosystem services.^{16–18} For example, body size in invertebrates influences predation rates and predator-prey preferences,^{19,20} while feeding mode in caddisflies affects a species' trophic position in aquatic food webs and their role as ecosystem engineers.²¹ Previous research has shown that functional diversity measures, which broadly describe the breadth of traits within communities, are

a better predictor of ecosystem services, including pollination and decomposition, than taxonomic measures such as species richness.^{9–12} This is because functional diversity directly accounts for differences between species that determine how ecosystem services are delivered. For example, seed set in pumpkins increases with increasing diversity of pollinator foraging preferences and body sizes.¹¹ Greater functional diversity is likely to be beneficial to ecosystem service provision as it decreases the likelihood of overlapping trait distributions, which is hypothesized to maximize resource exploitation through niche complementarity.^{22,23} While most studies focus on mesocosm scale or local patterns of functional diversity,^{8–12,24} functional diversity at macroecological scales (regional or national) determines the pool of effects traits available for local communities.²⁵ Therefore, as highlighted in studies of biodiversity and ecosystem functioning,^{25,26} macroecological patterns in functional diversity can provide key insights into the broader scale vulnerability of ecosystem functioning with ongoing biodiversity change. Our current lack of understanding of such large-scale and long-term trends hampers efforts to inform mitigation strategies to conserve ecosystem service provision.²⁷



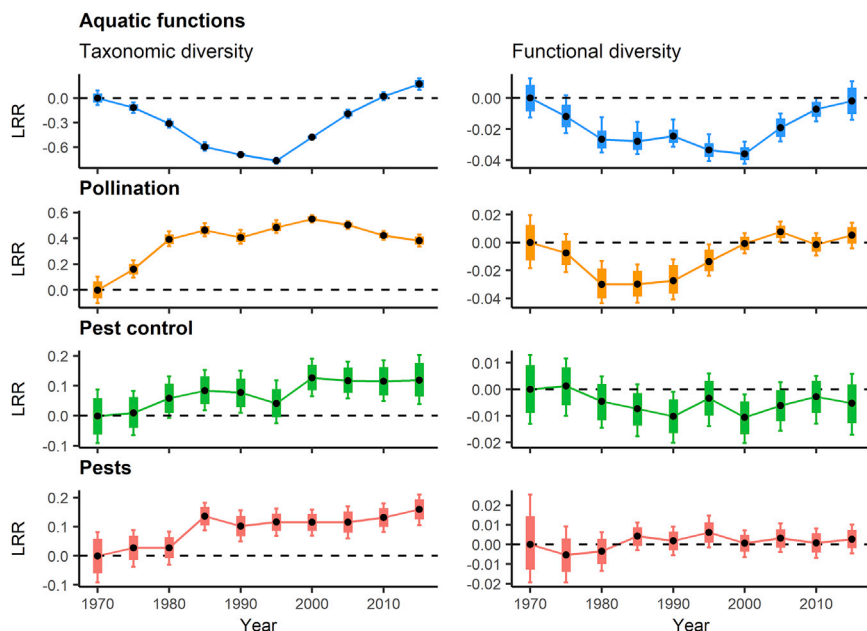


Figure 1. Trends in taxonomic diversity and functional diversity across Great Britain from 1970 to 2015 for species supporting each ecosystem service/disservice

Diversity measures were calculated for invertebrate species supporting aquatic functions (based on 92 species), pollination (based on 45 species), pest control (based on 68 species), and pests (based on 21 species). Trends are given as log response ratios (LRRs) compared to the mean value for 1970. Points show the mean, thick bars 80% credible interval (CI), and thin bars 95% CI. Bars for 1970 show uncertainty around the mean estimate for that year.

(where n is the number of traits), in which the position of each species is defined by its trait values.^{39–41} For each service/disservice we defined a distinct set of traits likely to underpin functional diversity important for ecosystem service provision. These included morphological measures (e.g., body size) and behavioral traits (e.g., the probability a bee species

To address this issue, we determined temporal trends in functional diversity and taxonomic diversity over a 45-year period at the scale of Great Britain for invertebrate species supporting three key ecosystem services and one disservice. We focused on invertebrate species supporting (1) crop pollination of oilseed rape, an economically important biofuel and oil crop²⁸ (using data for 45 bee species); (2) natural pest control, valued at £2.3 million p.a. alone for South East England²⁹ (using data for 68 predatory beetle species); and (3) aquatic functions including organic matter breakdown and substrate stabilization^{30–32} (using data for 92 caddisfly species). To provide a measure of an ecosystem disservice, we assess (4) invertebrate pests of arable crops and fruit plants that are known to directly cause declines in crop yields or quality (using data for 21 species).^{33,34} For the species supporting our four services/disservice, we used outputs from Bayesian occupancy models that predicted national scale trends in species occupancy across Great Britain from 1970 to 2015.³⁵ This is a time period characterized by significant shifts in anthropogenic drivers of biodiversity change, particularly pollution and agricultural practices.^{36,37} The occupancy models used spatially and temporally explicit records of species occurrence collated at the UK Biological Records Centre, a repository of tens of millions of records collected by naturalists for over 85 taxonomic groups.³⁸ Here, the occupancy corresponds to a proportion of occupied 1 km × 1 km sites across Great Britain.³⁵

Trends in taxonomic and functional diversity

For the species supporting each ecosystem service, we used the mean Great Britain level occupancy as a measure of taxonomic diversity comparable in interpretation to species richness. It is possible to represent the variation in species' traits as a multivariate space where species with similar trait values would be clustered together. By combining the occupancy estimates with morphological and behavioral functional effects trait data, we use this approach to construct n -dimensional hypervolumes

would make contact with an oilseed rape flower stigma) (the full list of traits and their justification for inclusion is included in Tables S1, S2, S3, and S4). From the hypervolumes, we estimated trends in functional dispersion (for simplicity we will refer to this as functional diversity), which measures the density and spread of occupancies within the functional trait space.⁴⁰ We used this as our focal measure of functional diversity, as it broadly captures niche complementarity and how different the species are within an assemblage based on their effects traits and, in our case, relative occupancies.^{40,42} We also assessed functional richness, which is the total volume of the hypervolume; this captures whether there has been a change in the amount of trait space driven most strongly by the loss or gain of certain trait combinations.⁴⁰ Yearly estimates of occupancy were available for each species,³⁵ however, due to long computational times when constructing hypervolumes, diversity measures were calculated at 5-year intervals between 1970 and 2015. All diversity measures are reported with 80% and 95% credible intervals representing uncertainty in occupancies for the individual species.

Over the 45-year period, we found patterns of decline and recovery in functional diversity for species supporting pollination and aquatic functions across Great Britain, whereas pest control agents and pests showed greater stability (Figure 1). For species supporting aquatic functions, we found a steep decline in taxonomic diversity and functional diversity between 1970 and 2000, followed by recovery in both diversity measures (Figure 1), whereas for pollinators, increases in taxonomic diversity over the start of the 45-year period were contrasted with declines in functional diversity (Figure 1). Functional diversity, which broadly captures niche complementarity, has been shown to maximize resource acquisition in aquatic invertebrate communities,^{43,44} as well as lead to increased pollination services by pollinator assemblages.^{9,11} Therefore, while we do not directly measure ecosystem service delivery, the functional

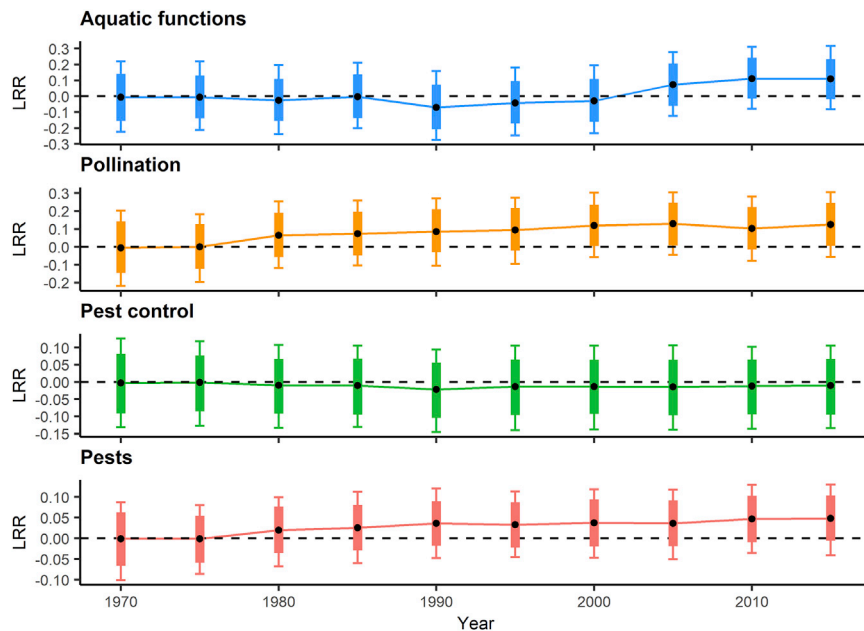


Figure 2. Trends in functional richness across Great Britain from 1970 to 2015 for species supporting each ecosystem service/disservice

Functional richness was calculated for invertebrate species supporting aquatic functions (based on 92 species), pollination (based on 45 species), pest control (based on 68 species), and pests (based on 21 species). Trends are given as log response ratios (LRRs) compared to the mean value for 1970. Points show the mean, thick bars 80% credible interval (CI), and thin bars 95% CI. Bars for 1970 show uncertainty around the mean estimate for that year.

diversity trends captured by our analysis highlight structural changes in species assemblages that are relevant to service delivery.

Interestingly, across all services, functional richness did not demonstrate any strong patterns of change (Figure 2). Therefore, our analysis suggests that it is unlikely that certain trait combinations were consistently lost from Great Britain, or novel trait combinations introduced to Great Britain over the period assessed. It is important to note that the absence of consistent changes in richness at the national level does not preclude the loss or gain of certain trait combinations at a local level.⁴⁵

Trends in taxonomic and functional composition

Taxonomic diversity and functional diversity do not provide information on changes in the identity of different species (taxonomic composition) and which traits are represented at different time periods (functional composition), respectively. Importantly, this means the same value of functional diversity may be derived from species assemblages that are functionally distinct and so support an ecosystem service in mechanistically different ways. To quantify this, we assessed compositional changes using Jaccard similarity relative to the baseline year of 1970 (the earliest record) for the same 5-year intervals. For taxonomic similarity, this was based solely on changes in species occupancies, and for functional similarity, this was assessed using the overlap of the hypervolumes.⁴⁰

While functional diversity in 2015 was not greatly different from 1970, we found directional changes in taxonomic and functional similarity compared with the 1970 baseline that persisted in 2015. For example, for species supporting pollination, functional diversity initially declined and then recovered after 2000, whereas there was no return to an equivalent level of functional similarity over the same period (Figures 1 and 3). This suggested that while the overall diversity of pollinator species traits had recovered in 2015, the trait space occupied by assemblages in

2015 was not identical to 1970. This is to say that pollinating species may have had similar net provision but were achieving it in functionally distinct ways. Similarly, for aquatic functions, the recovery observed in functional diversity was not accompanied by a strong increase in similarity (Figures 1 and 3). We even found directional changes in functional similarity for pests, despite relatively stable levels of functional diversity over the 45-year period (Figures 1 and 3). Shifts in functional composition, which captures changes in the dominant traits expressed by these species assemblages, could have led to functionally different ecosystem service provision in 2015 compared with 1970 (Figures 1 and 3).

Pest control agents showed the most stable functional composition, as there was little decline in functional similarity, despite strong declines in taxonomic similarity (Figure 3). Where taxonomic and functional compositional changes are decoupled is an indication of high functional redundancy.⁴⁵ As functional redundancy is a key component of resilience,^{46–48} predators of agricultural pests may have been the most resilient to environmental change over the period assessed. In contrast, pollination and aquatic functions were more likely to be vulnerable to perturbation, due to the combination of strong deviations in the functional diversity trends and declines in similarity.

Processes of change

The functional structure of species assemblages can be shaped by stochastic processes, which would lead to changes in species assemblages irrespective of their traits, or deterministic processes, where environmental conditions or biotic interactions lead to specific trait patterns.^{49,50} We used null models, which randomized traits across species, to see if we could detect deterministic processes of change in species assemblages over time.^{49,50} For species supporting aquatic functions and pollination, we found at certain points over the 45-year period functional diversity was lower than expected; this effect was strongest where we observed the greatest declines in functional diversity for these services (Figures 4A–4D). This suggests that, at these time points, changes in functional diversity were driven by deterministic processes, such as environmental filtering, leading to species assemblages becoming dominated (in terms of occupancy) by functionally similar species (Figures 4A–4D).

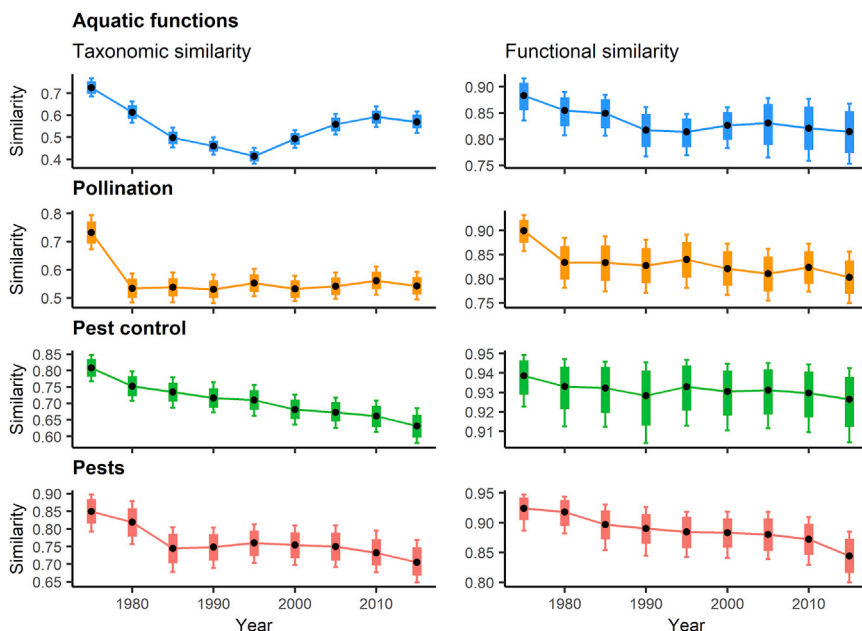


Figure 3. Taxonomic and functional similarity across Great Britain from 1975 to 2015 for species supporting each ecosystem service/disservice

Similarity was measured as the Jaccard index and calculated for invertebrate species supporting aquatic functions (based on 92 species), pollination (based on 45 species), pest control (based on 68 species), and pests (based on 21 species). Taxonomic similarity measures compositional changes based solely on the species occupancies and functional similarity measures compositional changes in the functional trait space. Changes in similarity are measured at 5-year intervals and compared to 1970. Decreasing similarity indicates directional compositional changes. Thick bars show 80% credible intervals (CI) and thin bars 95% CI and indicate the uncertainty around the estimate.

For pest control agents, despite no strong trends in the functional diversity measures, we did find that functional richness and diversity tended to be higher than expected based on our null models (Figures 4E and 4F). It is possible that the process of limiting similarity, whereby biotic factors (e.g., competition) stop species from being too functionally similar, may be determining the structure of pest control species assemblages.⁵¹ For pests, we found no clear evidence for deterministic processes shaping community structure based on the functional diversity measures (Figures 4G and 4H).

DISCUSSION

Our analyses of functional diversity and composition provide an important baseline for understanding how biodiversity change could impact ecosystem service provision at national scales. Changes in functional diversity at large spatial scales are likely to impact macroecological complementarity; for example, a loss of functional diversity at a national scale means that at any given location species are more likely to be functionally similar due to a reduced trait pool.²⁵ This could impact local ecosystem functioning through the direct loss of particular trait combinations reducing niche complementarity and impact regional ecosystem service provision where functioning is driven by heterogeneity in effects traits across space.²⁵ We focus on interspecific trait variation in our analysis; however, intraspecific variation (e.g., in response to landscape characteristics^{52,53}) has been found to have an equal or greater impact on ecosystem process than interspecific effects.⁵⁴ Unfortunately, appropriate data do not exist to investigate this aspect of functional diversity at the national scale.

For species supporting pollination services, we found contrasting patterns in taxonomic and functional diversity between 1970 to 1990. A number of studies highlight the potential for mismatches in taxonomic and functional diversity often in response to anthropogenic drivers of biodiversity change.^{55–57} Here we show

the potential for the relationship between these two diversity measures to be subject to change over long time periods. Both taxonomic and functional diversity are useful for defining complementary dimensions of biodiversity. For example, communities may undergo large-scale shifts in taxonomic composition, but not necessarily exhibit strong functional changes, as we found for the similarity measures for species supporting pest control. Traits are often selected with a specific function in mind; therefore, the lack of change in functional composition for the context in which it is being assessed (e.g., carabids as pest control agents) does not mean that changes in species composition are not important for other contexts or other ecosystem processes (e.g., carabids as prey items for other animals).

In the current analysis we do not attempt to determine the drivers that underpin our patterns of either taxonomic or functional biodiversity change; however, there have been large shifts in policy and land use that may partially explain the major trends.^{36,37,58} For example, where we observed the recovery of functional diversity for aquatic functions after 2000 follows the introduction environmental legislation across the EU aimed at improving wastewater treatment during the 1990s.^{36,58–60} Similarly, the increase in pollinator taxonomic diversity and concomitant decline in functional diversity between 1970 and 1990 coincides with the unprecedented expansion of oilseed rape coverage across Great Britain.⁶¹ This led to increases in occupancy of short-tongued generalist bee species, despite the widespread loss of more specialist bee pollinators associated with non-crop habitats.^{13,62}

Understanding how ecosystem services are fluctuating through time will be key to mitigating some of the most severe impacts of biodiversity change.⁶³ While the long-term large-scale monitoring of endpoint services, such as pollination rates in crops and subsequent yield information, represents a gold standard for understanding risks to ecosystem service provision, this does not currently exist.⁶⁴ Without such assessments, early indication of the disruption or alteration of important ecosystem processes resulting from anthropogenic-induced shifts in species assemblages may go undetected or be over-

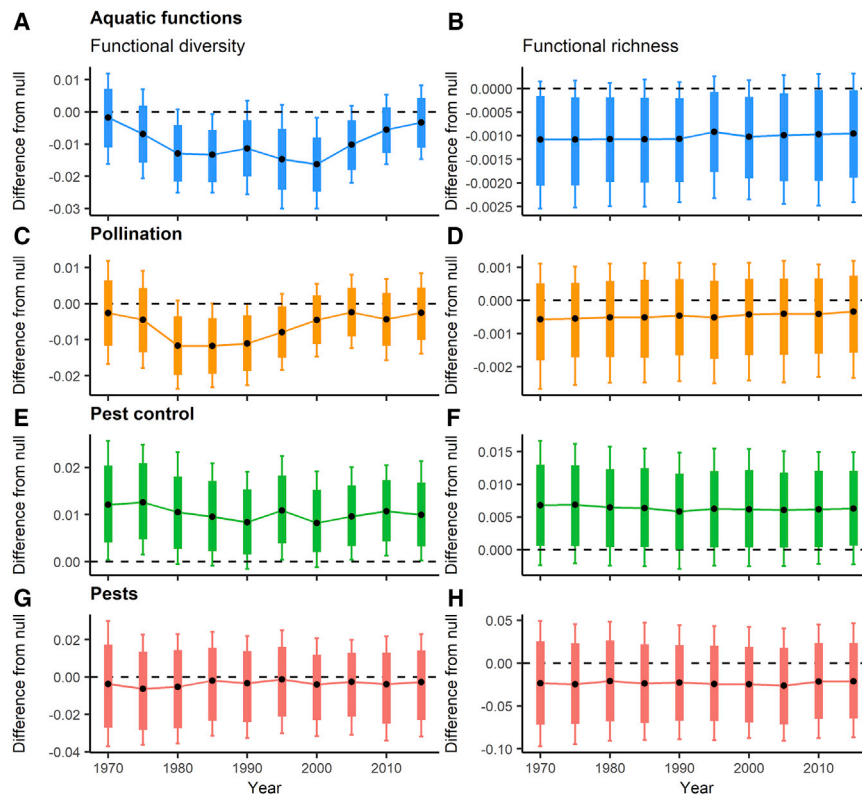


Figure 4. Difference between the observed and null (species traits randomized across occupancies) values of functional diversity and functional richness for species supporting each ecosystem service/disservice
This was used to detect deterministic processes of community assembly for species supporting aquatic functions (based on 92 caddisfly species) (A and B), pollination (based on 45 bee species) (C and D), pest control (based on 68 beetle species) (E and F), and pests (based on 21 invertebrate species) (G and H). Points show the mean, thick bars 80% credible interval (CI), and thin bars 95% CI.

underestimated. Here we show how functional diversity can provide insights into mechanistic changes in species assemblages linked to ecosystem services to help bridge this current knowledge gap. An important next step is linking long-term patterns in functional diversity to specific drivers of biodiversity change. While we focus on broader scale patterns based on the breadth of traits within invertebrate assemblages, linking individual effects traits with response traits, which are characteristics that determine how a species responds to their environment,^{17,65} could be used to provide detailed insights into the vulnerability of key ecosystem services to specific anthropogenic drivers of biodiversity change.⁶⁶

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- **KEY RESOURCES TABLE**
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- **QUANTIFICATION AND STATISTICAL ANALYSIS**

- Analysis of temporal trends and assembly processes
- Null models to determine assembly processes

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2021.07.080>.

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AUTHOR CONTRIBUTIONS

A.G., N.J.B.I., and B.A.W. conceived of the idea; A.G., N.J.B.I., F.K.E., and B.A.W. collated data; A.G. and N.J.B.I. analyzed the data; and all authors contributed to the writing and revision of the final manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
All data and code	This paper	https://doi.org/10.5281/zenodo.5101130
Occupancy estimates	³⁵	https://doi.org/10.1038/s41597-019-0269-1
Software and algorithms		
R version 3.6.2 on Platform: x86_64-w64-mingw32/x64 (64-bit)	The R Foundation for Statistical Computing	https://www.r-project.org/
R studio Version 1.2.5033	R studio	https://www.rstudio.com/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Arran Greenop (arrgre@ceh.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

The R code and the data used to produce the results and figures has all been deposited at <https://doi.org/10.5281/zenodo.5101130>.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We sought data relevant to ecosystem functions that could impact human wellbeing in either a positive or a negative way. Using these criteria we focused on three positive services: (i) pest control provided by predatory or omnivorous beetles that show an association with arable agriculture (pest control), (ii) bees associated with oilseed rape pollination (pollination), and, (iii) caddisflies, which provide a number of keystone aquatic ecosystem functions, including nutrient cycling and substrate stabilization (collectively labeled aquatic functions).¹⁴ We also looked at one negative service, (iv) the herbivory of arable crops and/or fruit trees that results in a direct reduction in yield or crop quality by invertebrate pest species (pests). We combined data on effects traits for these groups with Great Britain scale species level occupancy estimates described in Outhwaite et al.³⁵ to construct *n*-dimensional hypervolumes.^{39–41} These hypervolumes were used to calculate trends in functional diversity and composition, which were compared to taxonomic trends based solely on the species occupancies.

Occupancy estimates

We utilized species level estimates of national annual occupancy.³⁵ The outputs generated by Outhwaite et al.³⁵ consist of national-scale annual occupancy estimates from 1970 to 2015 for 5,293 species, in which occupancy corresponds to proportion of occupied 1km x 1km sites. Outhwaite et al.³⁵ provided occupancy estimates for both the UK and Great Britain: we use the latter, as they were available for all the species we included. These were subsetted for: 1) caddisflies supporting a range of aquatic ecosystem services; 2) bee species known to pollinate oilseed rape; 3) carabid and coccinellid species providing natural pest control in arable systems; and 4) pest species of arable crops and fruit trees. The choice of these species is described below. These estimates were derived from datasets of biological records collected by national recording schemes and analyzed using occupancy-detection models. Biological records consist of observations of species at a known time and location. In the UK, many recording schemes collate biological records for numerous taxonomic groups that are collected by volunteers (<https://www.brc.ac.uk/recording-schemes>). Due to the ad hoc nature of the data collection process, which does not follow a standardized protocol, these data are known to exhibit certain biases such as uneven recording intensity and imperfect detection.⁶⁷ It is possible to account for these biases using statistical approaches within an occupancy modeling framework.⁶⁸ Since the models were run in a Bayesian framework, the outputs consisted of a posterior distribution, enabling the uncertainty of occupancy estimate to be accounted for. Here, we use 1000 samples from the posterior distribution of each species' occupancy to calculate taxonomic diversity, functional diversity and similarity measures. The uncertainty in national scale diversity measures thus captures uncertainty in occupancies for the individual species and in the data generation process.

Functional traits supporting ecosystem services and disservices

We collected effects traits for the species supporting each service. These are morphological or behavioral characteristics that describe the impact of an organism on the ecosystem services (outlined in detail below).¹⁷ For all species included in analysis and their trait categorisations, see [Data S1](#), [S2](#), [S3](#), and [S4](#).

Aquatic functions

To assess changes in aquatic ecosystem functioning we focused on caddisflies (Trichoptera), which are responsible for multiple ecosystem services in aquatic environments, including substrate stabilization and nutrient cycling.^{14,32,69} We included 92 species of caddisflies in our analysis based on the presence of those species within the occupancy records in Outhwaite et al.³⁵ and trait information available from Usseglio-Polatera et al. and Tachet et al.^{70,71} The effects traits for caddisflies described their feeding habits, food preferences, locomotion modes and body size (see [Table S1](#) for the effects traits and their justification for inclusion in analysis). Thirteen out of the 92 caddisfly had species level trait information while the remaining functional trait data was at genus level (See [Data S1](#) for the trait resolution for each caddisfly species). The traits were broken down into individual categories and were fuzzy coded either 0 to 3 or 0 to 5 to show a species affinity for each category. To facilitate analysis the fuzzy coding was transformed to a proportion affinity for each species for each individual trait category using the *ade4* package in R.^{72,73}

Pollination

We focused on pollinators of oilseed rape, a globally important crop produced for biofuels and edible vegetable oils.²⁸ Oilseed rape is partially wind pollinated, but yields have found to be maximized through insect mediated pollination and can be positively affected by the species richness and functional diversity of pollinator communities.^{9,74,75} We included 45 bee species (Apidae) that pollinate oilseed rape⁶² for which we had occupancy trends and used traits derived from Woodcock et al.,^{9,76} Williams et al.,⁷⁷ and Bommarco et al.⁷⁸ Effects traits in the context of pollination were multiple morphological and behavioral traits that determine interactions with oilseed rape flowers and pollination success, including: mean time on flower, hairiness, probability of pollen on the body and probability of stigma contact (See [Table S2](#) for all traits). Note some of the traits were at the genus level (See [Data S2](#) for the trait resolution for each bee species).

Pest control

To assess pest control ecosystem services we focused on predatory or omnivorous ground beetle (Carabidae) and ladybird (Coccinellidae) species that predominantly hunt aphids, as these species play an important role in natural pest control in temperate arable agriculture.³³ We selected carabid species based on their inclusion in the Farm Scale Evaluation (FSE) dataset,⁷⁹ which contains carabid species lists for over 200 arable fields across the UK. We only included species for which there were complete occupancy records and trait information. This led to the inclusion of 63 ground beetle species and five ladybird species that are ubiquitous across the UK. The effects traits for pest control described diurnalism, habitat zone, body size and trophic position (see [Table S3](#) and [Data S3](#)).

Pests

The first three groups could be viewed to provide positive services to humans. In the final group, we considered temporal trends in species that have a negative impact. We identified crop pest species using Ellis et al.,³³ Alford,³⁴ ADHB,⁸⁰ and Hill⁸¹ and only included species that are considered major or frequent pests, had available life history information and occupancy records included in Outhwaite et al.³⁵ Overall, 21 pest species were included that attacked arable crops and fruit trees. The effects traits for pest species described the crops attacked, the part of the crop attacked and body size (see [Table S4](#) for all traits).

METHOD DETAILS

Diversity and similarity measures

Taxonomic diversity and similarity

Taxonomic diversity was the mean GB level species occupancy for each service calculated at 5-years intervals between 1970-2015. Taxonomic diversity describes the overall change in each service based solely on changes in the occupancies and does not account for the functional role of a species. To determine whether taxonomic diversity showed compositional changes over the time period we used the Jaccard similarity index. The similarity between two years i and $i+1$ for n species was calculated as:

$$\text{Total similarity} = 1 - \frac{B + C}{A + B + C} \quad (\text{Equation 1})$$

where A is $\sum_{k=1}^n \min(o_{k,i}, o_{k,i+1})$ (o_i and o_{i+1} represent vectors of occupancies for n species in the years i and $i+1$, respectively); B is $\sum_{k=1}^n (o_{k,i} - o_{k,i+1})$ only for species where $o_i > o_{i+1}$ and C is $\sum_{k=1}^n (o_{k,i+1} - o_{k,i})$ only for species where $o_{i+1} > o_i$. Alternatively, this can be expressed as:

$$\text{Total similarity}(\text{Ruzickaindex}) = \frac{\sum_{k=1}^n \min(o_{k,i}, o_{k,i+1})}{\sum_{k=1}^n \max(o_{k,i}, o_{k,i+1})} \quad (\text{Equation 2})$$

which simplifies to Jaccard in presence-absence cases.^{82,83} We used 1970 as the baseline for similarity measures as this was the earliest records we had. Similarity was calculated using the R package *adespatial*.⁸⁴

Functional diversity and similarity

For the species supporting each ecosystem service we calculated functional diversity measures using n -dimensional hypervolumes constructed through Gaussian kernel density estimation (KDE).^{39–41} Hypervolumes represent multidimensional functional space constructed using independent axes, in our case functional traits.^{39,41} Because the traits used contained categorical and continuous variables (see [Data S1](#), [S2](#), [S3](#), and [S4](#)) we applied a Gower dissimilarity matrix to the functional traits matrices, which were then subjected to principle coordinate analysis (PCoA).⁴⁰ We retained PCoA axes where the cumulative amount of variation explained was > 80% (up to a maximum of five axes were retained); these axes were then used as synthetic traits within hypervolume construction.⁴⁰ Each species was replicated by its occupancy estimate multiplied by 100. Thus, species with a higher occupancy had a greater weight in hypervolume construction.^{39,40} An important parameter in hypervolume delineation is the bandwidth, which could be viewed as the area for which the density of occupancies around a point is measured.³⁹ Because we were carrying out temporal comparisons the bandwidths for each axis were estimated and fixed on the value for 1970 (our earliest record).⁸⁵ Bandwidth was estimated using the Silverman Bandwidth estimator.³⁹ As stochastic points are used in the estimation of hypervolumes we set the seed to 1 for the random number generator for each hypervolume construction.³⁹ This meant that a hypervolume constructed using the same occupancy estimates two times in a row would lead to identical measures of functional diversity. Due to long computational times involved with constructing hypervolumes across all the services for each of the 1000 iterations of occupancies, we only calculated hypervolumes based on the occupancies at five-year intervals. Principle coordinate analysis was carried out in the *ade4*⁷² package and hypervolumes constructed using the *hypervolume*^{39,41} and *BAT*^{40,86} packages in R Studio.^{73,87}

The hypervolumes were used to calculate functional dispersion (for simplicity referred to as functional diversity), which is the average distance between the hypervolume centroid and a sample of stochastic points and represents the density and spread of the occupancies in trait space.⁴⁰ We used this as our focal measure of functional diversity as it broadly accounts for niche complementarity,⁴² which has been shown to be important in maximizing ecosystem service provision.^{8,9,11,44} We also calculated functional richness, which is the total volume of the hypervolume and represents the total amount of trait space.⁴⁰ The loss or gain of certain trait combinations from functional space would have the greatest impact on functional richness.^{40,42} We also calculated Jaccard similarity to measure changes in functional composition. For the functional similarity measures, using [Equation 1](#), A is the intersection between hypervolumes for the years i and $i+1$, B is the functional space unique to i and C is the functional space unique to $i+1$.⁴⁰

QUANTIFICATION AND STATISTICAL ANALYSIS

Analysis of temporal trends and assembly processes

For taxonomic diversity and functional diversity measures we calculated log response ratios by dividing each estimate by the mean value for 1970. This approach meant trends in diversity were described by deviations from zero to represent either increases or decreases since 1970. It also allows the diversity estimates to be put on a relative scale. From the 1000 posterior draws we calculated the mean value and 80% and 95% credible intervals, which reflect the uncertainty in our estimations for a given year ([Figure 1](#) and [2](#)). Error is included in the baseline (1970) by comparing all 1970 estimates to the mean for 1970. We also calculated the mean and same credible intervals for the similarity measures. As the similarity estimates describe compositional changes compared to the baseline of 1970, we present summary statistics from 1975–2015 ([Figure 3](#)). It is worth noting that our analysis does not account for abundance (or biomass), an important driver of ecosystem services,^{8,9,88} as long-term temporal trends in abundance are not available for the range of species included over the time period. Generally, there is a positive relationship between abundance and occupancy.⁸⁹ However, using occupancy estimates may fail to detect declines or increases in the abundance of widespread species, as abundance can decline without a complete loss of occupancy.⁹⁰ Thus, our estimates of changes in functional diversity are likely to be conservative.

Null models to determine assembly processes

Effects traits are not used to explicitly determine species characteristics that could affect a species response to its environment, however traits related to feeding and body size can influence an organisms response to certain environmental drivers.¹⁶ Therefore, we used null models to understand whether, particularly where we observed strong changes in functional diversity, we could find any evidence to suggest these changes were driven by deterministic processes, such as competition or environmental filtering at a national scale.⁴⁹ For every iteration of the occupancy estimates we randomly shuffled the rows of the functional trait matrices across species (identical to shuffling species labels) and calculated expected values for the functional diversity measures.⁹¹ The expected values were then subtracted from the observed values. This gave us a posterior distribution for the difference between expected and observed functional diversities from which we calculated the mean value and 80% and 95% credible intervals ([Figures 4A–4H](#)). For the functional diversity measures values greater than zero indicate deterministic process that limit the functional similarity of species, which can be caused by biotic interactions such as competition.^{49,51} Values less than zero suggest abiotic factors, such as environmental filtering, are dominant in shaping communities and lead to greater functional similarity between species.⁴⁹ The credible intervals were used to infer either weak (80%) or strong evidence (95%) for these deterministic processes for all diversity the measures.