



## Research article

## Effects of future agricultural change scenarios on beneficial insects

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## ABSTRACT

Insects provide vital ecosystem services to agricultural systems in the form of pollination and natural pest control. However, there are currently widespread declines in the beneficial insects which deliver these services (i.e. pollinators and 'natural enemies' such as predators and parasitoids). Two key drivers of these declines have been the expansion of agricultural land and intensification of agricultural production. With an increasing human population requiring additional sources of food, further changes in agricultural land use appear inevitable. Identifying likely trajectories of change and predicting their impacts on beneficial insects provides a scientific basis for making informed decisions on the policies and practices of sustainable agriculture.

We created spatially explicit, exploratory scenarios of potential changes in the extent and intensity of agricultural land use across Great Britain (GB). Scenarios covered 52 possible combinations of change in agricultural land cover (i.e. agricultural expansion or grassland restoration) and intensity (i.e. crop type and diversity). We then used these scenarios to predict impacts on beneficial insect species richness and several metrics of functional diversity at a 10km (hectad) resolution. Predictions were based on species distribution models derived from biological records, comprising data on 116 bee species (pollinators) and 81 predatory beetle species (natural enemies).

We identified a wide range of possible consequences for beneficial insect species richness and functional diversity as result of future changes in agricultural extent and intensity. Current policies aimed at restoring semi-natural grassland should result in increases in the richness and functional diversity of both pollinators and natural enemies, even if agricultural practices remain intensive on cropped land (i.e. land-sparing). In contrast, any expansion of arable land is likely to be accompanied by widespread declines in richness of beneficial insects, even if cropping practices become less intensive (i.e. land-sharing), although effects of functional diversity are more mixed.

## 1. Introduction

Beneficial insects deliver a wide variety of ecosystem services essential to human life (Schowalter et al., 2018). In agricultural systems, two of the most economically important services are pollination and natural control of crop pests (by predatory or parasitic 'natural enemies'). Pollination services have been valued at US\$235–577 billion (Lautenbach et al., 2012) and affect yield or quality of most globally important crop types (Klein et al., 2007; Gallai et al., 2009), whilst natural control of crop pests has been valued at over US\$400 billion (Costanza et al., 1997) and is vital to many high economic value crops (e.g. Colloff et al., 2013; Classen et al., 2014).

There is increasing evidence of widespread declines in both pollinators (Kluser and Peduzzi, 2007; Potts et al., 2010; Ollerton et al.,

2014; Powney et al., 2019) and natural enemies (Kotze and O'Hara, 2003; Brooks et al., 2012; Oliver et al., 2015). A significant contributor to these declines has been the expansion of agricultural land and the intensification of agricultural production (Robinson and Sutherland, 2002; Kotze and O'Hara, 2003; Kluser and Peduzzi, 2007; Potts et al., 2010), with the accompanying prevalence of agrochemicals (Basedow, 1990; Woodcock et al., 2016) and simplification of landscapes (Kotze and O'Hara, 2003; Bianchi et al., 2006b; Ollerton et al., 2014; Senapathi et al., 2015; Landis, 2017). As insects themselves decline, so do the services they provide (Kremen et al., 2002; Oliver et al., 2015) such that deficits are either already occurring (Garibaldi et al., 2011; Zhao et al., 2015a, 2015b) or predicted in the near future (Aizen et al., 2008).

With an increasing human population requiring additional sources of food (Godfray et al., 2010), further changes in agricultural land use

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appear inevitable. Simultaneously, international (CBD, 2017) and national (Defra, 2011, 2018) policies incorporate significant commitments toward the restoration of intensively managed agricultural land. Future agricultural landscapes may therefore develop in many possible ways to meet these multiple goals. One of the most obvious distinctions is the contrast between 'land-sharing' and 'land-sparing' approaches (Green et al., 2005; Ekroos et al., 2016). Land-sharing integrates food production and biodiversity conservation on the same land, increasing the amount of farmed land but reducing intensity of agriculture. Land-sparing segregates food production and biodiversity conservation, compensating for a reduction in the farmed area by intensifying farming practices. Assessing the relative sustainability of these options, in terms of both food production and environmental impact, relies on empirical and theoretical knowledge of how changes in agricultural systems affect populations of beneficial insects, especially at the regional and national scales at which most agricultural policy is targeted and formulated. The majority of studies documenting the impacts of agriculture on beneficial insects have focused on the past (e.g. Robinson and Sutherland, 2002; Kotze and O'Hara, 2003; Brooks et al., 2012; Comont et al., 2014; Senapathi et al., 2015). While this provides evidence that the expansion of intensive agricultural practices has had largely negative impacts on beneficial insects, it has limited value in planning future agricultural policy, with comparatively few studies exploring potential future impacts over larger spatial scales (Reidsma et al., 2006). Furthermore, individual species differ in terms of functional characteristics that affect their capacity to exploit their environment. These differences affect not only on their response to environmental change but also in their capacity to deliver ecosystem services (Greenop et al., 2018; Woodcock et al., 2019). Exploring how changes in the occurrence of individual species impact on the functional diversity of the insect community thus provides additional information on how future agricultural changes may affect the capacity of beneficial insects to deliver ecosystem services (Hoehn et al., 2008; Greenop et al., 2018; Woodcock et al., 2019).

Here we develop national-scale scenarios of future change in the extent and intensity of agricultural land use to understand potential impacts on beneficial insects. The aim of scenario approaches is not to predict the future, but to better understand the range of potential outcomes, uncertainties and trade-offs between different responses (Moss et al., 2010; Holway et al., 2012). They provide a valuable method for engaging with policy makers (Audsley et al., 2006) and stakeholders (Tompkins et al., 2008) and a route for operationalising the ecosystem service concept into land use policy (Grêt-Regamey et al., 2017). Creating exploratory scenarios and modelling their impacts on key service indicators such as beneficial insect communities can thus be an important tool for designing and refining land use policy options (Holway et al., 2012), especially if these approaches can be based on widely available data and accessible models. The aims of this study were therefore:

- i) To create multiple exploratory scenarios of potential future change in the extent of agricultural land cover and intensity of land use at national scale for Great Britain (GB)
- ii) To use biological records to model the effect of existing patterns of land cover and land use on the distributions of pollinators (bees) and natural enemies (predatory beetles)
- iii) To use these models to predict the impacts of all possible combinations of the scenarios on the species richness and functional diversity of beneficial insects

## 2. Methods

### 2.1. Creating scenarios of future agricultural change

#### 2.1.1. Scenarios of agricultural land cover extent

We created two contrasting scenarios to explore changes in the extent of agricultural land, the balance between arable vs. pastoral

farming, and the relative amounts of improved (i.e. intensively managed with agrochemical inputs and sowing of productive grass species) vs. semi-natural (i.e. retaining a diverse plant community and with low levels of management) grasslands:

- i) Expansion of land under agricultural production. This was primarily driven by conversion of improved grassland to arable, with a smaller proportion from conversion of semi-natural grasslands to improved grassland (Fig. 1). Such changes may occur under increased need for food production (Godfray et al., 2010) and demands to keep farming profitable (Defra, 2018).
- ii) Restoration of grassland (i.e. retraction of agricultural land), converting improved grassland to semi-natural and arable to improved grassland (Fig. 1), in line with national (Defra, 2018) and international (European Commission, 2011) policies for restoring semi-natural grasslands. Although GB semi-natural grasslands do have an agricultural role (extensive grazing) they are rare in the intensive arable systems which dominate Western Europe (Pedro Silva et al., 2008).

Expansions were performed in sequential fashion, with 5% increments up to 30% change from the baseline (i.e. present-day land cover from the CEH Land Cover Map 2007 (LCM2007, Morton et al., 2011), creating scenarios with varying levels of expansion (Fig. 1). Because GB is already dominated by agricultural land (Morton et al., 2011) expansions beyond 30% are unlikely. For the grassland restoration scenario, expansions of up to 30% are sufficient to cover the ambition of 500,000 Ha of "additional wildlife-rich habitat" set out by Defra (2018). Our scenarios focussed on large scale changes if all other factors (e.g. climate, population growth) were to remain constant.

Scenarios were modelled using the Integrated Valuation of Ecosystem Services and Trade-offs (InVEST) Rule Based Scenario Generator tool (v3.3.3 Sharp et al., 2017). InVEST is a free, open-source suite of ecosystem service models (Sharp et al., 2017). The scenario generator tool ('the tool' from hereon) is a spatially explicit, multi-criteria, multi-objective evaluation tool (Tenerelli and Carver, 2012) for generating user-defined scenarios of land cover or land use change. The tool determines relative suitability between grid cells for change by spatial overlay of multiple criteria provided by the user (Sharp et al., 2017). The parameters required by the tool are described in Table 1 for each land cover change scenario.

Transition likelihoods for the first scenario were parameterised by extrapolation of observed 20th century land cover changes. These were calculated by comparing the 1930s Dudley Stamp land utilisation map (Stamp, 1931) and LCM2007, both at 1 km resolution, determining the relative frequency of transitions between land cover classes and weighting transition likelihoods accordingly. The second scenario was more hypothetical, there having been no large scale grassland reversion in GB since the agricultural depression of the late 19th century (Best and Coppock, 1962). Instead, the purpose of this scenario was to offer a contrast to agricultural expansion, assuming prioritisation of habitat restoration and biodiversity conservation.

The tool combines all parameter values (Table 1) via a weighted sum to gain an index of suitability per cell for each different land cover class. Cells are then converted sequentially, from most to least suitable, until the required level of change is met. Where two or more cells are of equal suitability, the tool selects at random. To assess uncertainty introduced by this random element, each scenario was run 100 times. Uncertainty was then quantified as the percentage of runs for which each cell was equal to its modal land cover across runs (see Supplementary Material, Appendix 2). To explore the sensitivity of the tool to the parameters and weightings, and to validate its ability to recreate known land cover change, we ran the tool using the 1 km version of the Dudley Stamp map as a baseline to examine which combination of parameters most closely approached the actual configuration of the LCM2007 (see Supplementary Material, Appendix 3).

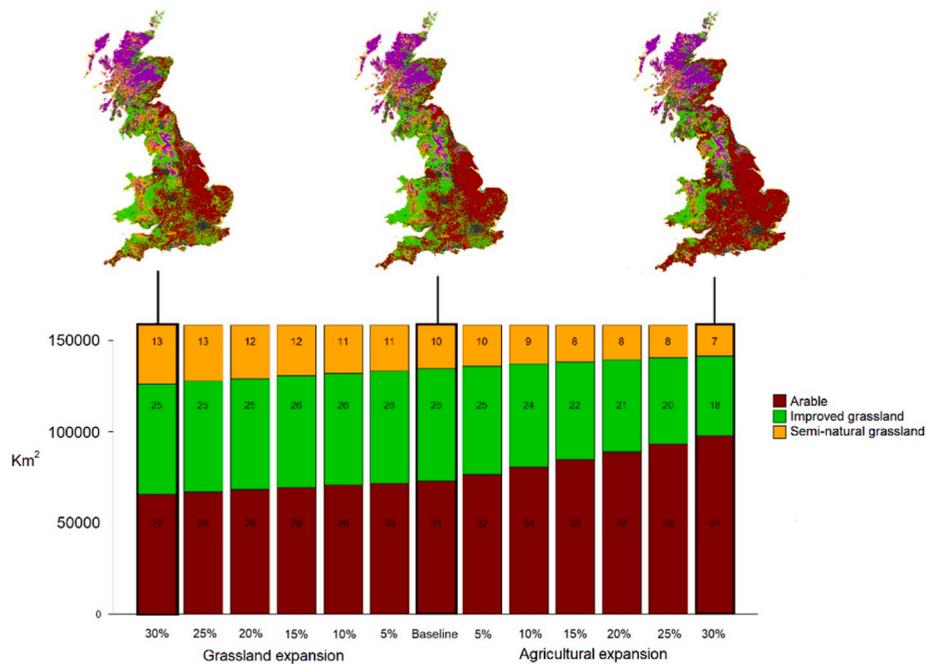


Fig. 1. Plot of areas of arable land, improved grassland and semi-natural grassland under each land cover scenario, and associated land cover maps for the baseline and two most extreme scenarios. Numbers on bars are percentage of GB covered by each land cover class under the scenario.

Table 1

Parameters of the InVEST scenario generator tool and the data used for inputs under each of the two land cover change scenarios.

Model parameter	Description	Input under each scenario	
		i. Agricultural expansion	ii. Grassland restoration
Baseline land cover	Raster map of land cover	CEH Land Cover map 2007 (LCM2007) at 1 km resolution (Morton et al., 2011), simplified to ten aggregate classes (broadleaved woodland, coniferous woodland, arable, improved grassland, semi-natural grassland, mountain/heath/bog, saltwater, freshwater, coastal, built up)	
Quantity of Change	Required change in each land cover class	5% increments up to 30% increase in area of agricultural land cover	5% increments up to 30% increase in total area of grassland
Transition Likelihood	Matrix giving likelihood of pairwise transitions between land cover types	Historic changes from comparison of land utilisation survey (Stamp, 1931) and LCM2007	Reverse of transitions used for scenario i
Priority	Relative priority of different land covers to break ties	Arable land > improved grassland	Semi-natural > improved grassland
Suitability Factors	Vector map of other known drivers of land suitability	Agricultural land classification (ALC, Soil Survey of Scotland Staff, 1981, MAFF, 1988, Natural England 2012, Welsh Government, 2017) giving suitability of land for different agricultural uses based on soils, topography and climate	
Proximity	Distance beyond which distance to existing cells ceases to affect suitability	Set to 10 km. This is beyond the size of most farm management units where proximity to existing land determines likelihood of change.	
Constraints	Vector map of factors constraining change	Sites of Special Scientific Interest. Basic unit of GB statutory land protection, known to prevent change over long timescales (Ridding et al., 2015).	Not used

2.1.2. Scenarios of agricultural land use intensity

We used crop type and rotation as a proxy for agricultural intensity per 1 km cell. Cropping patterns drive many aspects of intensity, including presence of monocultures, levels of agrochemical inputs, degree of landscape simplification and available resources for biodiversity. Because cropping patterns are highly variable over time and influenced by complex drivers such as market forces, government policies and societal preferences (Li et al., 2018) we did not use the approach of extrapolating from historic trends. Instead, we classified cropping patterns from an annual satellite-derived map of GB crops, CEH Land Cover® plus: Crops (CEH, 2016). We used 3 years of data (2015–2017) to assign each 1 km cell to one of three broad cropping classes ('intensive', 'diverse' or 'extensive') using a simple rule base (Supplementary Material, Table S1).

In general, cells with a predominance of winter-sown cereals and oilseed rape were considered 'intensive' because growing these crops without others in the rotation generally requires substantial use of synthetic pesticides and fertilisers (Sieling and Christen, 2015) and is

associated with increased mechanisation and homogeneous landscapes. These two crops have dominated GB agriculture over recent decades, with detrimental effects on biodiversity (Robinson and Sutherland, 2002).

Cells with a large variety of crops or a predominance of root or legume crops, were considered 'diverse'. Such landscapes are likely to show larger numbers of crop types over time as many of these crops can only be grown as part of more complex rotations. We follow the general usage of 'crop diversification' as cultivation of multiple crop types in a given area (Gurr et al., 2016; Aizen et al., 2019) rather than necessarily indicating structural heterogeneity or diversity in its ecological sense.

A prevalence of spring cereals or temporary grass leys was considered indicative of extensive agriculture. Spring sown cereals are generally beneficial for biodiversity in comparison to winter crops (Dicks et al., 2019) and often require lower inputs of pesticides (Robinson and Sutherland, 2002), whilst the prevalence of temporary grass is likely to be indicative of farming systems utilising rotational pest and soil management and thus a reduced reliance on agrochemicals.

We constructed three scenarios, based on expansion of one of the three cropping classes into all areas where the ALC indicated the land was suitable to do so. A fourth scenario kept cropping patterns at their present-day baseline. We also predicted cropping intensity for cells which may become arable under one of the land cover change scenarios by taking the modal cropping class for all arable cells on land of the same ALC grade within 100 km. Any cell which was dominated by arable land under the selected land cover scenario then received the appropriate cropping class from the selected cropping scenario. Our scenarios did not account for configuration of crops within the landscape. Although this is known to affect beneficial insect communities (e.g. Martin et al., 2016; Hass et al., 2018; Haan et al., 2019; Sirami et al., 2019) we cannot predict the composition of a given landscape within a 1 km cell using our scenario methods.

## 2.2. Modelling responses of beneficial insects

To provide data on GB beneficial insect populations, we used biological records (i.e. records submitted to voluntary recording schemes, a form of ‘citizen science’). These provide large volumes of data on species’ identification, date and location (hereafter ‘occurrence’ data) and are a valuable resource for analysing large-scale patterns in time and space (Powney and Isaac, 2015).

Occurrence data on bees at 1 km resolution were extracted from the databases of the Bees, Wasps and Ants Recording Society held by the UK Biological Records Centre (BRC). The predominance of bees in pollination of GB crops is well supported (Garratt et al., 2014). For natural enemies, we focussed on carabid and coccinellid beetles. These are well-studied in agricultural systems (e.g. Cole et al., 2002; Woodcock et al., 2010; Comont et al., 2014; Woodcock et al., 2014) and sufficiently well-recorded to have large volumes of species-level data (unlike other natural enemy groups, e.g. parasitoid wasps). We compiled lists of predatory carabids and aphidophagous coccinellids (see Supplementary Material, Table S7 for references used to identify diets) and obtained occurrence data held by BRC from the Ground Beetle Recording Scheme and UK Ladybird Survey, respectively. Data were cleaned to remove species and data that might lead to erroneous or biased results (see Supplementary Material, Appendix 4 for data cleaning steps), resulting in 116 bee species, 16 coccinellids and 65 carabids for analysis (full list in Supplementary Material, Tables S5 and S6).

We used species distribution models (SDMs) to model the relationships between species occurrence and current patterns of land cover and agricultural intensity. SDMs are widely used to determine and make predictions from the relationships between occurrence and environmental variables (Elith and Leathwick, 2009). SDMs were based on the ten LCM2007 aggregate land cover classes, with arable land subdivided into the current three cropping intensity types. They also included three climatic variables to ensure that modelled distributions were influenced by climatic constraints. These were mean January and July temperatures and mean annual precipitation, averaged across 2000–2012 at 1 km resolution (Robinson et al., 2017). A logistic regression based SDM was run for each species of beneficial insect, with all land cover/use and climate variables included as standardised, explanatory variables. The models are thus of the form:

$$\text{logit}(\text{Pr}(\text{Occ})) = \alpha + \beta_1 \text{LULC}_1 + \beta_2 \text{LULC}_2 + \beta_3 \text{LULC}_3 + \dots + \beta_{10} \text{LULC}_{10} + \beta_{\text{TJan}} \text{TJan} + \beta_{\text{TJul}} \text{TJul} + \beta_{\text{Prec}} \text{Prec}$$

Where  $\text{Pr}(\text{Occ})$  is the probability of occurrence,  $\alpha$  is the intercept and  $\beta$  is the regression coefficient for each covariate. Preliminary analysis supported logistic regression as performing as well as other, more analytically complex methods (Supplementary material, Appendix Table S4), as also demonstrated in previous studies (Bradter et al., 2018). Models were run in R (v3.4.0 R Core Team, 2017) using *Zoon* (August et al., 2017; Golding et al., 2017), with 1000 random background pseudoabsences and 5-fold cross-validation. Because spatial

variation in recorder effort influences the probability that lack of occurrence indicates a genuine absence (Lobo et al., 2010) we used a threshold of species detection (Hickling et al., 2006; Redhead et al., 2015), with only cells with at least one other species permitted as pseudoabsences. See Supplementary Material (Table S4 & Fig. S1) for preliminary analyses used to determine this threshold.

## 2.3. Predicting scenario impacts on species richness and functional diversity

Relationships with land cover and cropping intensity derived from the SDMs were then used to predict the occurrence of each species in each  $10 \times 10$  km grid cell (hectad) for all factorial combinations of land cover and cropping intensity scenarios (52 possible combinations = 2 land cover change scenarios  $\times$  6 expansion steps  $\times$  4 cropping intensity scenarios + 3 cropping intensity scenarios at baseline land cover + 1 baseline land cover and current cropping patterns). Climate layers were held constant across scenarios. For each scenario combination, occurrence probabilities were summed per hectad across species, giving an index of relative richness (Scherrer et al., 2018).

Functional diversity was calculated from traits compiled from sources listed in Supplementary Material, Table S5. Traits included body size (total length of thorax/elytra and intertegular distance (Cane, 1987) for beetles and bees, respectively) because it is related to many functional roles including foraging range (Greenleaf et al., 2007), dispersal ability (Gutiérrez and Menéndez, 1997) and life history (Peters and Peters, 1986). For natural enemies we also included wing length (macropterous, brachypterous or dimorphic) as this is indicative of dispersal ability (Den Boer, 1970) and thus species’ vulnerability to disturbance and ability to exploit new habitats (Kotze and O’Hara, 2003). We also included diet breadth (oligolectic or polylectic for pollinators; omnivore, generalist or specialist predator for natural enemies), which indicates both responses (vulnerability to changes in food resource availability) and effects (likelihood of feeding on species relevant to agricultural systems). For pollinators, which are highly seasonal in their life cycles, we also included seasonality (voltinism and flight season duration). We calculated two metrics of functional diversity for each hectad based on the species predicted to be found there under each scenario. These were: 1) Rao’s quadratic entropy (RaoQ), which expresses the average difference in functional traits between two randomly selected individuals from a community, as calculated from average abundance-weighted pairwise trait differences between species (Botta-Dukát, 2005); 2) functional evenness ( $F_{\text{Eve}}$ ), which provides a measure of the evenness of species functional trait distribution (Mason et al., 2005). These two metrics were chosen because of their relative simplicity for calculation over large numbers of hectad and scenario combinations, and their representation of different aspects of functional diversity (Mason et al., 2005; Petchey and Gaston, 2006; Mouchet et al., 2010). We also calculated community-weighted mean body size to directly explore one of the traits driving functional diversity responses. Body size is typically inter-correlated with many other characteristics (Gaston and Blackburn, 1996; Gutiérrez and Menéndez, 1997; Greenleaf et al., 2007; Rusch et al., 2015) and thus provides a core single-trait metric of community functional composition. Functional diversity metrics were calculated using the *FD* package (Laliberté and Legendre, 2010; Laliberté et al., 2014) and used predicated probability of occurrence from SDMs to weight traits in lieu of data on relative abundance (Woodcock et al., 2014).

## 3. Results

Under the baseline land cover and cropping scenarios, we found that our response metrics of species richness and functional diversity were generally inter-correlated to some extent (correlations with species richness were  $-0.79$ ,  $0.46$  and  $-0.88$  for pollinators and  $-0.58$ ,  $0.65$ ,  $-0.71$  for natural enemies, for each of RaoQ,  $F_{\text{Eve}}$  and community-

weighted body size, respectively; Spearman’s rho,  $n = 2659$ ,  $p < 0.001$  in all cases). Although these correlations are statistically significant across the entire dataset of all GB hectads, it was clear that a wide variation in functional diversity metrics per hectad is possible for any given value of species richness (Supplementary Material, Fig. S3). We therefore present results for species richness and each functional diversity metric separately.

### 3.1. Impacts of land cover scenarios

The expansion of agricultural land cover had almost uniformly negative impacts on species richness, with declines in some hectads exceeding 20% (Fig. 2A and B). These were generally proportional to the degree of expansion, although there was some indication that these declines levelled off at higher percentage expansions. Effects on functional diversity were more mixed. For pollinators, roughly equivalent numbers of hectads showed increases and decreases in RaoQ whilst  $F_{Eve}$  was more consistently negatively affected (Fig. 2A). For natural enemies, both metrics tended to show decreases, as for species richness. In terms of community-weighted body size, arable expansion tended to favour larger-bodied pollinators and smaller-bodied natural enemies.

The grassland restoration scenario (Fig. 2C and D) was generally beneficial for species richness with widespread increases of up to 10% and very few decreases. The effect on all metrics of functional diversity was generally positive for natural enemies (Fig. 2D), whilst for pollinators 10–20% of hectads showed decreases of <1% in RaoQ (Fig. 2C). Community-weighted mean body size responded in the inverse manner to agricultural expansion, with a trend towards smaller-bodied pollinators and larger-bodied natural enemy communities.

### 3.2. Impacts of cropping intensity scenarios

The intensification scenario had little impact on pollinators, with roughly equal numbers of hectads showing increases and decreases of <1% for most metrics (Fig. 3A). Natural enemies were slightly more prone to negative impacts, especially in terms of RaoQ, although these changes were still small (Fig. 3B). The diversification scenario was similar in its impacts, with impacts being generally negative but slight (Fig. 3C and D). In contrast, the extensification scenario had much more

pronounced effects (Fig. 3E and F). These included widespread increases of up to 10% in beneficial insect species richness and RaoQ. Functional evenness tended to show strong decreases under the extensification scenario for both beneficial insect groups. Effects of the extensification scenario on community-weighted mean body size differed between pollinators and natural enemies - for pollinators (Fig. 3E) results varied widely between hectads, but for natural enemies there were widespread increases in community-weighted mean body size by up to 10% (Fig. 3F).

### 3.3. Impacts of scenario combinations

There were 52 possible combinations of the land cover and cropping intensity scenarios. Note, some of these are not necessarily plausible, but are included to provide a full characterisation of the range of potential futures. Results are shown for all in Supplementary Material, Figs. S4–S8. We present here scenarios relating to land-sharing or -sparing practises attempting to find trade-offs between the extent and intensity of agricultural land.

Extensification had some mitigating effect on the negative impacts of agricultural expansion under the sharing scenario (Fig. 4A and B). However, at higher levels of expansion this was insufficient to prevent widespread declines in richness in hectads converted from other land uses to extensive agriculture. This was true despite some increases in hectads which were already agricultural but became less intensive (Fig. 5C and G). RaoQ generally increased under land-sharing, whilst  $F_{Eve}$  showed strong decreases. Community-weighted mean body size increased for both insect groups, contrasting with their opposite responses to the agricultural expansion scenario.

The land-sparing example (Fig. 4C and D) showed more widespread increases in species richness. These were often less pronounced (<1%) than under the land-sharing scenario but were not countered by declines in other hectads (Fig. 5D and H). RaoQ showed a mixture of small increases and small decreases for pollinators and predominantly small increase for natural enemies. The effect on  $F_{Eve}$  was generally positive for both groups. Land-sparing retained the effect of grassland restoration on community-weighted mean body size, with shifts towards smaller-bodied pollinator and larger-bodied natural enemy communities.

Individual species varied widely in their responses to each scenario

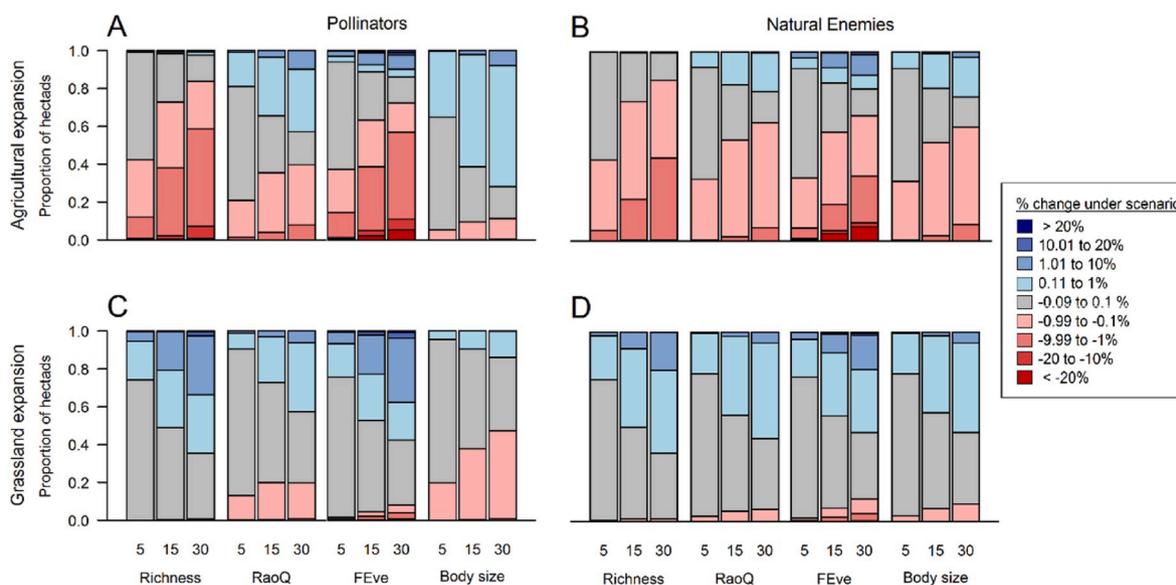
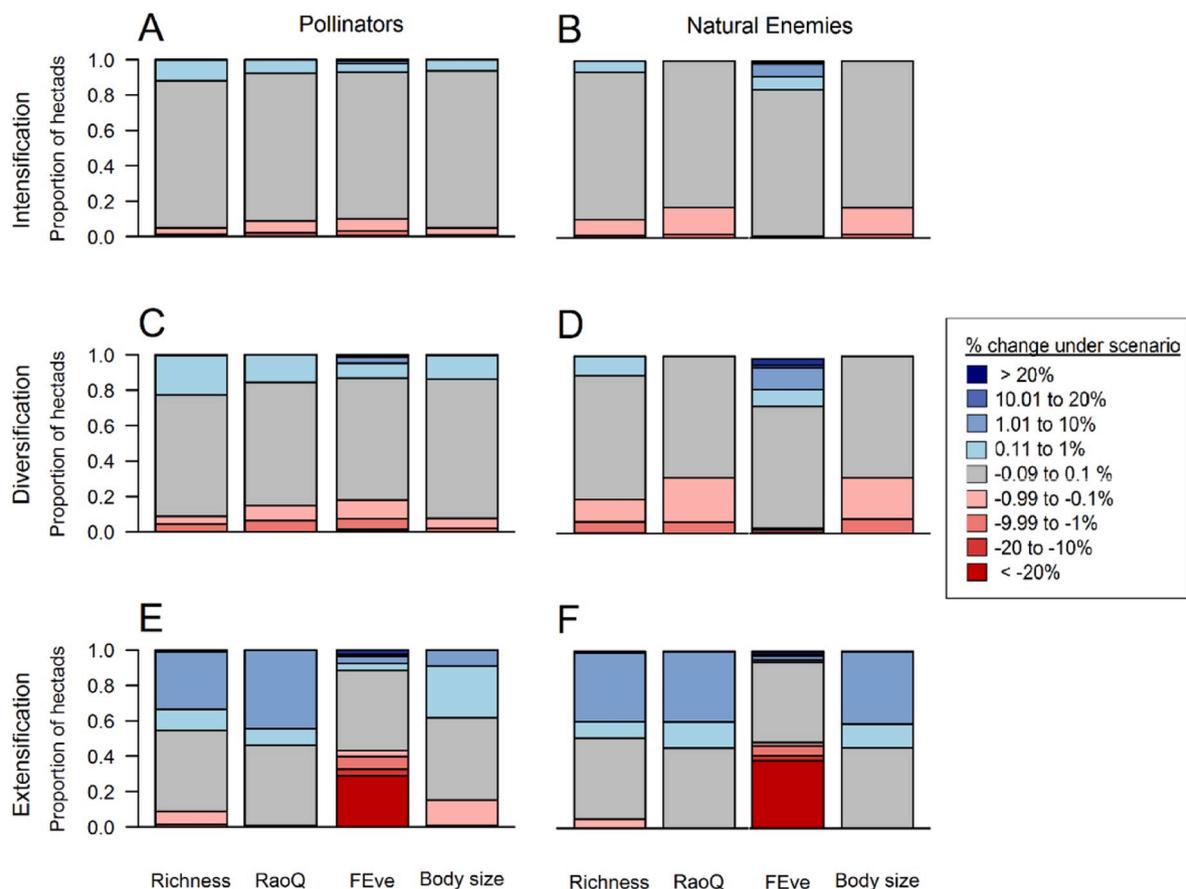


Fig. 2. Plots showing proportions of GB hectads with different levels of percentage change in species richness and functional diversity metrics under three levels of the two land cover expansion scenarios; agricultural expansion (A, B), and grassland restoration (C, D). Results are shown for pollinators (A, C) and natural enemies (B, D). Results for all levels of expansion are presented in Supplementary Material, Figs. S4–S7. RaoQ = Rao’s quadratic entropy, FEve = functional evenness, Body size = community-weighted mean body size.



**Fig. 3.** Plots showing proportions of GB hectads with different levels of percentage change in species richness and functional diversity metrics under the three cropping intensity scenarios; intensification (A, B), diversification (C, D) and extensification (E, F). Results are shown for pollinators (A, C, E) and natural enemies (B, D, F). RaoQ = Rao's quadratic entropy, FEve = functional evenness, Body size = community-weighted mean body size.

(Supplementary material, Fig. S8), including species which appeared to benefit from generally detrimental scenarios such as high levels of agricultural expansion or intensification.

### 3.4. Exploring model uncertainty and performance

Exploring uncertainty by re-running scenarios 100 times showed a mean 76% agreement with the modal class across all scenarios, for cells which showed change in any scenario run (Supplementary material, Table S1). Uncertainty was affected by spatial resolution, being relatively high in the assignment of some individual 1 km cells whereas land cover patterns at coarser resolutions or regional scales were more conserved across scenario re-runs. SDM performance was generally better for pollinating bees than for natural enemies (Supplementary Material, Table S8) but performance for both groups was sufficient to imply confidence in their predicative ability under the scenarios.

## 4. Discussion

### 4.1. Impacts of the scenarios on beneficial insect species richness and functional diversity

#### 4.1.1. Scenarios of land cover change

Our results show that gains in agricultural production from increases in the area of agricultural land are likely to be accompanied by widespread detrimental impacts on beneficial insect species richness, in line with well-known detrimental impacts of conversion of semi-natural grasslands to agriculture on beneficial insect communities (Kremen et al., 2002; Kotze and O'Hara, 2003; Ollerton et al., 2014; Senapathi

et al., 2015). Whilst many areas of GB showed moderate decreases, the consequences for individual hectads may be more severe, with species richness losses of over 20%. Effects on functional diversity were rather more mixed, especially for pollinators. Where there are correlations between traits driving the response to land use change and those used to calculate functional diversity (Williams et al., 2010) it is probable that functional diversity will respond differently to species richness. In our case, traits such as body size, dispersal ability and diet breadth all mediate the responses of beneficial insects to landscape. Indeed, our results showed a shift in communities towards large-bodied pollinators (e.g. *Bombus* spp.) under agricultural expansion. This is in agreement with the findings of Bommarco et al. (2010) that small generalists are particularly sensitive to habitat loss. Larger pollinators tend to have longer foraging ranges (Greenleaf et al., 2007) and are thus better able to tolerate the fragmentation of resources imposed by highly agricultural landscapes (Woodcock et al., 2014), although they may be more susceptible to land use intensification in other contexts (Rader et al., 2014). There is ample evidence that certain pollinator communities do occur preferentially in agriculturally dominated landscapes (e.g. Holzschuh et al., 2013; Redhead et al., 2018; Powney et al., 2019). Expansion of these functionally-similar species can either increase functional diversity, when they arrive in landscapes where these functions were previously underrepresented, or reduce it where these communities replace or dominate one with greater functional diversity, hence the mixed results for pollinators. For natural enemies, functional diversity tended to decrease in line with species richness, suggesting either that natural enemies with a wider range of functions are reduced by agricultural expansion or that those species which do benefit from agricultural expansion are even more functionally homogenous than for

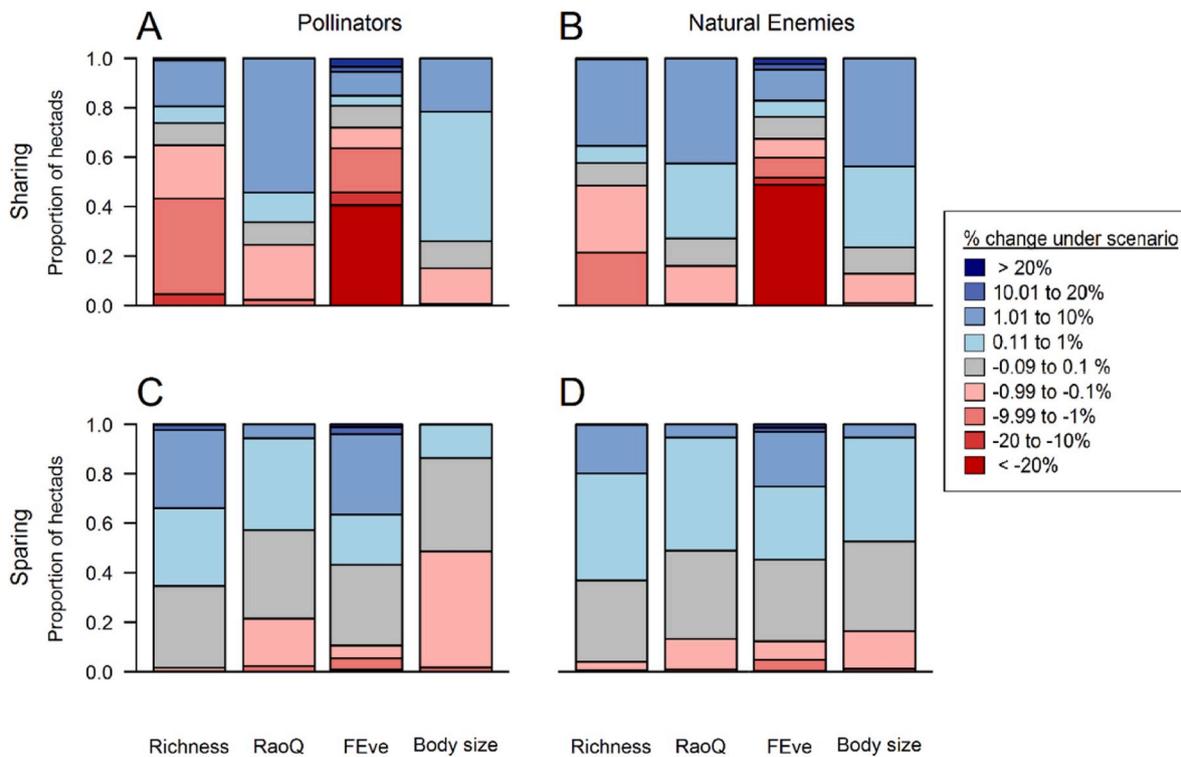


Fig. 4. Plots showing proportions of GB hectads with different levels of percentage change in species richness and functional diversity metrics under land-sharing (30% expansion of agricultural land and extensification of cropping, A, B) and land-sparing (30% restoration of grassland and extensification of cropping, C, D). Results are shown for pollinators (A, C) and natural enemies (B, D). Results for all possible scenario combinations are presented in Supplementary Material, Figs. S4–S7. RaoQ = Rao’s quadratic entropy, FEve = functional evenness, Body size = community-weighted mean body size.

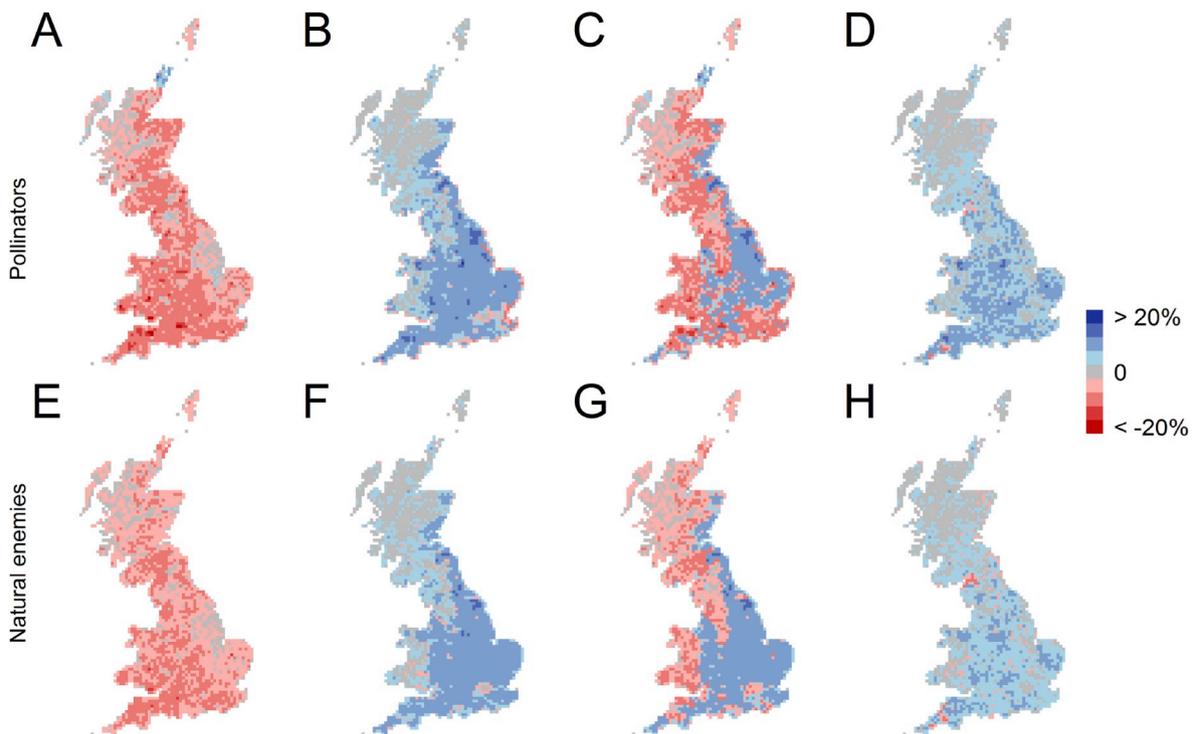


Fig. 5. Examples of percentage change in species richness for pollinators (A–D) and natural enemies (E–H) under different scenario combinations. Scenarios are: 30% expansion of agricultural land and intensification of cropping (A, E); 30% restoration of grasslands and extensification of cropping (D, H); 30% expansion of agricultural land and extensification of cropping (land-sharing, C, G); 30% restoration of grasslands and intensification of cropping (land-sparing, D, H).

pollinators. Compared to pollinators, many carabid and coccinellid natural enemies are less mobile and more closely linked to local habitat (Woodcock et al. 2010, 2014) so, although there are species which are more frequent in agricultural landscapes, it is possible that the constraint of ability to survive in such landscapes on function is even more severe. This reduction in functional diversity is important, as a recent meta-analysis found functional diversity in predator communities to be a significant predictor of their capacity to provide natural pest control (Greenop et al., 2018). The decrease in community-weighted natural enemy body size is supported by observations that larger predatory carabids (e.g. *Carabus* spp.) are particularly vulnerable to agricultural land uses (Ribera et al., 2001; Cole et al., 2002) and observed declines linked to their reduced dispersal and lower reproductive rates (Kotze and O'Hara, 2003).

Grassland restoration was generally beneficial for both pollinators and natural enemies. Expansions of 15–20%, corresponding to the targets of international (European Commission, 2011) and national (Defra, 2018) biodiversity strategies, resulted in an average increase of 0.71–0.96% of pollinators and 0.33–0.45% natural enemies per hectad, with individual hectads showing up to 22% and 10% increases in pollinator and natural enemy richness, respectively. It is unsurprising that restoration of semi-natural grasslands has positive impacts on both groups, given the known importance of these habitats (Cole et al., 2002; Woodcock et al., 2014; Carrié et al., 2017; Holland et al., 2017). This scenario also had generally positive effects on all metrics of functional diversity, suggesting that grassland restoration benefits a functionally broad range of beneficial insects. The restoration of semi-natural grassland can be a very long-term process in terms of effective reconstruction of the target community (Walker et al., 2004; Redhead et al., 2014). That said, restored grassland can still show significant increases in biodiversity over much shorter timescales than those required to return to a pre-disturbance state (Török et al., 2010; Redhead et al., 2014) and the LCM2007 semi-natural grassland class does not consist solely of pristine examples. Therefore, the scenario does not assume full restoration, suggesting localised benefits for beneficial insect richness and functional diversity even at low to moderate levels of change.

#### 4.1.2. Scenarios of cropping intensity

Scenarios of cropping intensity generally had less pronounced impacts than land cover change, when applied in isolation. This is as expected, given that these are effectively proxies for the crops and management regimes in the agricultural landscape and are therefore modifying the management intensity of a given land cover rather than changing it completely. The effect of the intensification scenario was particularly limited, perhaps because the species which have demonstrably survived in GB's already highly-modified agricultural landscapes are likely to be able to persist even if these landscapes are managed more intensively (Redhead et al., 2018). The impact of the crop diversification scenario was similarly low. However, recent studies have found that habitat configuration or heterogeneity may be more important than crop diversity per se (Hass et al., 2018; Redlich et al., 2018) or that the effect of crop diversity has complex interactions with configurational diversity and the amount of semi-natural habitat in the landscape (Sirami et al., 2019). Because of the limited number of crops and uneven distribution of agricultural land quality in GB, cropping regimes identified as being 'diverse' under our rule base are mostly in parts of the country with relatively highly modified agricultural landscapes (e.g. root crop systems in the East of England). For many species, the association between occurrence and diverse cropping as modelled by the SDMs is thus likely to be biased towards negative.

The extensification scenario had more pronounced effects on species richness and functional diversity, reflecting a more profound change from the predominant agricultural systems of GB. For richness and RaoQ these were positive. Extensification was the only scenario to show an opposite effect for  $F_{Eve}$  to RaoQ, with a large proportion of hectads showing strong decreases in  $F_{Eve}$ . Unlike RaoQ, functional evenness is

particularly sensitive to species present at low levels (Mason et al., 2005) and outlying trait values, especially where these appear in combination (Májeková et al., 2016). Extensification may thus promote a subset of species with relatively extreme trait values. Examining which species show the greatest expansions under extensification to shows these to include small, oligolectic bees with localised distributions (e.g. *Panurgus banksianus*, *Heriades truncorum*) and small, predatory beetles (e.g. *Notiophilus* spp.).

#### 4.1.3. Scenario combinations

When scenarios were applied in combination it was clear that the differing responses to land cover and cropping intensity resulted in a wide range of possible outcomes. In some cases, there was a degree of trade-off between species richness and functional diversity. Attempting to mitigate against the detrimental impacts of agricultural expansion by decreasing the intensity of agriculture (i.e. land-sharing) appeared to help maintain or even increase RaoQ, but strong decreases in species richness and  $F_{Eve}$  were still widely evident. This scenario also created a strong polarisation between existing agricultural areas which showed increases in richness as they became less intensively used and areas which were converted to agriculture and thus experienced strong decreases.

Combining restoration of grassland with an intensification of remaining agriculture to maintain overall levels of food production (i.e. land-sparing) generally only slightly reduced the positive impacts of grassland restoration on species richness and functional diversity. Other studies have also found land-sparing is often determined to be preferable in terms of maximising biodiversity benefits, even when considered alongside delivery of crop yield (Kamp et al., 2015; Ekroos et al., 2016; Finch et al., 2019; Lamb et al., 2019), but few of these have examined functional diversity. It should also be borne in mind that the delivery of ecosystem services from both pollinators and natural enemies is strongly driven by landscape composition (Bianchi et al., 2006a; Chaplin-Kramer et al. 2011, 2013; Martin et al., 2016; Holland et al., 2017), so landscapes which venture too far down the route of segregating habitats for biodiversity and crop production may end up undermining the delivery of these services to crops.

#### 4.2. Limitations of the methods

Our scenario approach has several limitations. The fate of individual 1 km cells under any one scenario should be treated with caution due to the degree of uncertainty evident at this scale (Sharp et al., 2017), although predictions from SDMs should be less affected since these are made at the hectad scale. Because our scenarios explored a wide range of potential alternative futures, we did not include predictions of climate change, which may potentially drive, exacerbate or mitigate against changes in land cover and land use intensity. Although our SDMs included climatic variables, and so could potentially take account of climate change, such scenarios would need to be timebound. This would require knowledge of the timescales over which changes in land cover and cropping systems occur. Since these can vary from gradual processes to step changes, as has been demonstrated by the complex history of agricultural land use change in GB (Best and Coppock, 1962; Ridding et al., 2015), parametric timebound scenarios is a complex task better suited to a narrower range of plausible futures driven by socioeconomic priorities (e.g. O'Neill et al., 2017). Whilst comparatively simplistic, our approach has the advantage of being transparent to the user. Because each individual scenario can be generated quickly, it becomes feasible to explore a wide range of scenarios focussed on plausible, near-future changes in agriculture at the national scale (Swinbank, 2017; Defra, 2018) with multiple iterations to obtain estimates of uncertainty. Our results thus are of particular relevance to policy makers in narrowing down land use policy targets and building stakeholder engagement and confidence (Holway et al., 2012). More complex approaches can then be deployed to further develop policies and determine how to

incentivise transitions towards a desired target.

Our use of SDMs also has its limitations. Whilst model performance was generally adequate, performance metrics suggested that many factors driving insect distributions were unaccounted for (e.g. landscape configuration, vegetation communities, soils, local land management). Predictions from SDMs also assume that relationships with current land uses classes are representative of future ones. For example, the areas we classified as 'diverse' may not reflect the actual outcomes of future agricultural diversification, which might include crops not currently grown in GB or novel agricultural practices such as intercropping. Future 'intensive' agriculture might also look very different to current intensive landscapes, especially if 'ecological intensification' approaches succeed in creating agricultural landscapes which both promote biodiversity and enhance crop yields via enhanced ecosystem service delivery (Bommarco et al., 2013; Pywell et al., 2015; Landis, 2017; Kleijn et al., 2019). Recent research has also identified that the extremes of land-sharing and land-sparing are both outperformed by combinations of spared land, high-intensity farmland and lower-intensity farmland (Finch et al., 2019). Whilst such approaches cannot be explored with our current suite of scenarios, our methods could be adapted to simulate these and explore their effects.

#### 4.3. Conclusions and implications for land use policy and ecosystem service delivery

Our results clearly show a range of possible consequences for beneficial insects depending on the future extent and intensity of agriculture. With declines in beneficial insects being an issue of global importance, and GB being at a pivotal time for determining future land use policy (Defra, 2018), it is particularly important to explore such potential futures explore the potential consequences of changes in land use and thus select and refine policy targets. Encouragingly, our results suggest that current policies aimed at increasing the area of semi-natural grassland should increase average richness and functional diversity of both pollinators and natural enemies. These increases are likely to occur even if agricultural practices are intensified, for species richness at least. In contrast, any expansion of arable land is likely to drive further declines in beneficial insect richness and functional diversity, even if agricultural practices become less intensive.

The relationships between species richness, functional diversity and ecosystem service delivery are complex (see overviews in Balvanera et al., 2006; Bianchi et al., 2006b; Balvanera et al., 2013). Ecosystem service delivery at fine scales can depend more on the abundance of key species (Griffin et al., 2013; Kleijn et al., 2015; Winfree et al., 2015; Woodcock et al., 2019), a factor we did not directly consider in the current analysis (Woodcock et al., 2019), than richness or diversity. Despite this complexity, richness and functional diversity of beneficial insects are increasingly found to be important at broader spatiotemporal scales (Hoehn et al., 2008; Greenop et al., 2018; Dainese et al., 2019; Woodcock et al., 2019). It is thus difficult to predict exactly how the changes resulting from our scenarios might affect the ecosystem services delivered by beneficial insects across GB agricultural systems. Whilst it is hard to assess the relative merits of situations which show trade-offs between species richness and functional diversity, avoiding situations that lead to severe declines in either would seem advisable.

The methods used in this study demonstrate a valuable approach to the creation of scenarios for land use change and the exploration of their impacts on biodiversity at national scale. By using widely available spatial datasets (e.g. land cover maps) and occurrence data from biological records, modelled via open-source software (e.g. R and InVEST) our results demonstrate that scenario exploration can be performed in an intuitive, transparent and interoperable manner (Holway et al., 2012) and show the value of these data and methods for providing policy-relevant information.

#### Declaration of competing interest

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

#### CRediT authorship contribution statement

**John W. Redhead:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing - original draft, Visualization. **Gary D. Powney:** Methodology, Software. **Ben A. Woodcock:** Methodology, Writing - review & editing. **Richard F. Pywell:** Conceptualization, Supervision, Funding acquisition.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2020.110550>.

#### References

- Aizen, M.A., Garibaldi, L.A., Cunningham, S.A., Klein, A.M., 2008. Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Curr. Biol.* 18, 1572–1575.
- Aizen, M.A., Aguiar, S., Biesmeijer, J.C., Garibaldi, L.A., Inouye, D.W., Jung, C., Seymour, C.L., 2019. Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Global Change Biol.* 25, 3516–3527.
- Audsley, E., Pearn, K.R., Simota, C., Cojocaru, G., Koutsidou, E., Rounsevell, M.D.A., Alexandrov, V., 2006. What can scenario modelling tell us about future European scale agricultural land use, and what not? *Environ. Sci. Pol.* 9, 148–162.
- August, T., Lucas, T., Golding, N., McNerny, G., 2017. Zoon: Reproducible, Accessible & Shareable Species Distribution Modelling. R package version 0.6. <https://github.com/zoonproject/zoon>.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156.
- Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., Griffin, J.N., 2013. Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. *Bioscience* 64, 49–57.
- Basedow, T., 1990. Effects of Insecticides on Carabidae and the Significance of These for Agriculture and Species Number. *The Role of Ground Beetles in Ecological and Environmental Studies*, pp. 115–125.
- Best, R.H., Coppock, J.T., 1962. *The Changing Use of Land in Britain. The Changing Use of Land in Britain.*
- Bianchi, F.J., Booij, C., Tschamtker, T., 2006a. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. Biol. Sci.* 273, 1715–1727.
- Bianchi, F.J.J.A., Booij, C.J.H., Tschamtker, T., 2006b. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. Biol. Sci.* 273, 1715–1727.

- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P., Öckinger, E., 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. Lond. B Biol. Sci.* 277, 2075–2082.
- Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28, 230–238.
- Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.* 16, 533–540.
- Bradter, U., Mair, L., Jönsson, M., Knape, J., Singer, A., Snäll, T., 2018. Can opportunistically collected Citizen Science data fill a data gap for habitat suitability models of less common species? *Methods Ecol. Evol.* 9, 1667–1678.
- Brooks, D.R., Bater, J.E., Clark, S.J., Monteith, D.T., Andrews, C., Corbett, S.J., Chapman, J.W., 2012. Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *J. Appl. Ecol.* 49, 1009–1019.
- Cane, J.H., 1987. Estimation of bee size using intertegular span (apoidea). *J. Kans. Entomol. Soc.* 60, 145–147.
- Carrié, R., Andrieu, E., Cunningham, S.A., Lentini, P.E., Loreau, M., Ouin, A., 2017. Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. *Ecography* 40, 85–97.
- CBD, 2017. Strategic Plan for Biodiversity 2011–2020, Including Aichi Biodiversity Targets.
- CEH, 2016. Land cover plus: crops. In: Hydrology, N.C.f.E., Ltd, R.S.A.C. (Eds.), NERC Centre for Ecology & Hydrology.
- Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14, 922–932.
- Chaplin-Kramer, R., de Valpine, P., Mills, N.J., Kremen, C., 2013. Detecting pest control services across spatial and temporal scales. *Agric. Ecosyst. Environ.* 181, 206–212.
- Classen, A., Peters, M.K., Ferger, S.W., Helbig-Bonitz, M., Schmack, J.M., Maassen, G., Steffan-Dewenter, I., 2014. Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. *Proc. Biol. Sci.* 281.
- Cole, L.J., McCracken, D.I., Dennis, P., Downie, I.S., Griffin, A.L., Foster, G.N., Waterhouse, T., 2002. Relationships between agricultural management and ecological groups of ground beetles (Coleoptera: carabidae) on Scottish farmland. *Agric. Ecosyst. Environ.* 93, 323–336.
- Colloff, M.J., Lindsay, E.A., Cook, D.C., 2013. Natural pest control in citrus as an ecosystem service: integrating ecology, economics and management at the farm scale. *Biol. Contr.* 67, 170–177.
- Comont, R.F., Roy, H.E., Harrington, R., Shortall, C.R., Purse, B.V., 2014. Ecological correlates of local extinction and colonisation in the British ladybird beetles (Coleoptera: coccinellidae). *Biol. Invasions* 16, 1805–1817.
- Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Paruelo, J., 1997. The value of the world's ecosystem services and natural capital. *nature* 387, 253–260.
- Dainese, M., Martin, E.A., Aizen, M., Albrecht, M., Bartomeus, I., Bommarco, R., Garibaldi, L.A., 2019. A Global Synthesis Reveals Biodiversity-Mediated Benefits for Crop Production. *bioRxiv* 554170. A Global Synthesis Reveals Biodiversity-Mediated Benefits for Crop Production.
- Defra, 2011. Biodiversity 2020: A Strategy for England's Wildlife and Ecosystem Services. Department for Environment, Food and Rural Affairs, London.
- Defra, 2018. A Green Future: Our 25 Year Plan to Improve the Environment (London).
- Den Boer, P.J., 1970. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). *Oecologia* 4, 1–28.
- Dicks, L.V., Ashpole, J.E., Dänhardt, J., James, K., Jönsson, A., Randall, N., Sutherland, W.J., 2019. Farmland conservation. In: Sutherland, W.J., Dicks, L.V., Ockendon, N., Petrovan, S.O., Smith, R.K. (Eds.), *What Works in Conservation* 2019. Open Book Publishers, Cambridge, UK, pp. 291–330.
- Ekroos, J., Odman, A.M., Andersson, G.K.S., Birkhofer, K., Herbertsson, L., Klatt, B.K., Smith, H.G., 2016. Sparing land for biodiversity at multiple spatial scales. *Frontiers Ecol. Evol.* 3.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Syst.* 40, 677–697.
- England, Natural, 2012. Agricultural Land Classification: Protecting the Best and Most Versatile Agricultural Land. Natural England.
- European Commission, 2011. Communication from the Commission to the European Parliament, the Council, the Economic and Social Committee and the Committee of the Regions: Our Life Insurance, Our Natural Capital: an EU Biodiversity Strategy to 2020 (Brussels).
- Finch, T., Gillings, S., Green, R.E., Massimino, D., Peach, W.J., Balmford, A., 2019. Bird conservation and the land sharing-sparing continuum in farmland-dominated landscapes of lowland England. *Conserv. Biol.* 0.
- Gallai, N., Salles, J.-M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* 68, 810–821.
- Garibaldi, L.A., Aizen, M.A., Klein, A.M., Cunningham, S.A., Harder, L.D., 2011. Global growth and stability of agricultural yield decrease with pollinator dependence. *Proc. Natl. Acad. Sci. Unit. States Am.* 108, 5909–5914.
- Garratt, M.P.D., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Potts, S. G., 2014. The identity of crop pollinators helps target conservation for improved ecosystem services. *Biol. Conserv.* 169, 128–135.
- Gaston, K.J., Blackburn, T.M., 1996. Rarity and body size: importance of generality. *Conserv. Biol.* 10, 1295–1298.
- Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Toulmin, C., 2010. Food security: the challenge of feeding 9 billion people. *Science* 327, 812–818.
- Golding, N., August, T.A., Lucas, T.C.D., Gavaghan, D.J., van Loon, E.E., McNerny, G., 2017. The zoon r package for reproducible and shareable species distribution modelling. *Methods Ecol. Evol. Publ. online.* <https://doi.org/10.1111/2041-210X.12858>.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. *Science* 307, 550–555.
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596.
- Greenop, A., Woodcock, B.A., Wilby, A., Cook, S.M., Pywell, R.F., 2018. Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis. *Ecology*.
- Grêt-Regamey, A., Sirén, E., Brunner, S.H., Weibel, B., 2017. Review of decision support tools to operationalize the ecosystem services concept. *Ecosystem Services* 26, 306–315.
- Griffin, J.N., Byrnes, J.E., Cardinale, B.J., 2013. Effects of predator richness on prey suppression: a meta-analysis. *Ecology* 94, 2180–2187.
- Gurr, G.M., Lu, Z., Zheng, X., Xu, H., Zhu, P., Chen, G., Heong, K.L., 2016. Multi-country evidence that crop diversification promotes ecological intensification of agriculture. *Nature Plants* 2, 16014.
- Gutiérrez, D., Menéndez, R., 1997. Patterns in the distribution, abundance and body size of carabid beetles (Coleoptera: caraboidea) in relation to dispersal ability. *J. Biogeogr.* 24, 903–914.
- Haan, N.L., Zhang, Y., Landis, D.A., 2019. Predicting landscape configuration effects on agricultural pest suppression. *Trends in Ecology & Evolution*.
- Hass, A.L., Kormann, U.G., Tschamtké, T., Clough, Y., Baillo, A.B., Sirami, C., Batáry, P., 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proc. Biol. Sci.* 285, 20172242.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biol.* 12, 450–455.
- Hoehn, P., Tschamtké, T., Tylanakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. Lond. B Biol. Sci.* 275, 2283–2291.
- Holland, J.M., Douma, J.C., Crowley, L., James, L., Kor, L., Stevenson, D.R.W., Smith, B. M., 2017. Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agron. Sustain. Dev.* 37, 31.
- Holway, J., Gabbe, C., Hebbert, F., Lally, J., Matthews, R., Quay, R., 2012. Opening access to scenario planning tools. *Policy Focus Report* 60.
- Holzschuh, A., Dormann, C.F., Tschamtké, T., Steffan-Dewenter, I., 2013. Mass-flowering crops enhance wild bee abundance. *Oecologia* 172, 477–484.
- Kamp, J., Urazaliev, R., Balmford, A., Donald, P.F., Green, R.E., Lamb, A.J., Phalan, B., 2015. Agricultural development and the conservation of avian biodiversity on the Eurasian steppes: a comparison of land-sparing and land-sharing approaches. *J. Appl. Ecol.* 52, 1578–1587.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Rader, R., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6.
- Kleijn, D., Bommarco, R., Fijen, T.P.M., Garibaldi, L.A., Potts, S.G., van der Putten, W.H., 2019. Ecological intensification: bridging the gap between science and practice. *Trends Ecol. Evol.* 34, 154–166.
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschamtké, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. Lond. B Biol. Sci.* 274, 303–313.
- Kluser, S., Peduzzi, P., 2007. Global Pollinator Decline: a Literature Review.
- Kotze, D.J., O'Hara, R.B., 2003. Species decline—but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135, 138–148.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. Unit. States Am.* 99, 16812–16816.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305.
- Laliberté, E., Legendre, P., Shipley, B., 2014. FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology. R package version 1.0-12. R Foundation for Statistical Computing, Vienna, Austria.
- Lamb, A., Finch, T., Pearce-Higgins, J.W., Ausden, M., Balmford, A., Feniuk, C., Green, R. E., 2019. The consequences of land sparing for birds in the United Kingdom. *J. Appl. Ecol.* 0.
- Landis, D.A., 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic Appl. Ecol.* 18, 1–12.
- Lautenbach, S., Seppelt, R., Liebscher, J., Dormann, C.F., 2012. Spatial and temporal trends of global pollination benefit. *PLoS One* 7, e35954.
- Li, S., Juhász-Horváth, L., Pintér, L., Rounsevell, M.D.A., Harrison, P.A., 2018. Modelling regional cropping patterns under scenarios of climate and socio-economic change in Hungary. *Sci. Total Environ.* 622–623, 1611–1620.
- Lobo, J.M., Jiménez-Valverde, A., Hortal, J., 2010. The uncertain nature of absences and their importance in species distribution modelling. *Ecography* 33, 103–114.
- MAFF, 1988. Revised Guidelines and Criteria for Grading the Quality of Agricultural Land Ministry of Agriculture, Fisheries and Food Agricultural Land Classification of England and Wales.
- Májeková, M., Paal, T., Plowman, N.S., Bryndová, M., Kasari, L., Norberg, A., de Bello, F., 2016. Evaluating functional diversity: missing trait data and the importance of species abundance structure and data transformation. *PLoS One* 11, e0149270.
- Martin, E.A., Seo, B., Park, C.R., Reineking, B., Steffan-Dewenter, I., 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecol. Appl.* 26, 448–462.

- Mason, N.W.H., Moullot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118.
- Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Simpson, I.C., 2011. Final Report for LCM2007 - the New UK Land Cover Map. NERC/Centre for Ecology and Hydrology.
- Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., Willbanks, T.J., 2010. The next generation of scenarios for climate change research and assessment. *Nature* 463, 747.
- Mouchet, M.A., Villéger, S., Mason, N.W.H., Moullot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* 24, 867–876.
- Oliver, T.H., Isaac, N.J., August, T.A., Woodcock, B.A., Roy, D.B., Bullock, J.M., 2015. Declining resilience of ecosystem functions under biodiversity loss. *Nat. Commun.* 6, 10122.
- Ollerton, J., Erenler, H., Edwards, M., Crockett, R., 2014. Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science* 346, 1360–1362.
- O'Neill, B.C., Krieger, E., Ebi, K.L., Kemp-Benedict, E., Riahi, K., Rothman, D.S., Kok, K., 2017. The roads ahead: narratives for shared socioeconomic pathways describing world futures in the 21st century. *Global Environ. Change* 42, 169–180.
- Pedro Silva, J., Toland, J., Jones, W., Eldridge, J., Thorpe, E., O'Hara, E., 2008. LIFE and Europe's Grasslands: Restoring a Forgotten Habitat. DG environment of the EU (LIFE unit-E4).
- Petchev, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9, 741–758.
- Peters, R.H., Peters, R.H., 1986. *The Ecological Implications of Body Size*. Cambridge University Press.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353.
- Powney, G.D., Isaac, N.J., 2015. Beyond maps: a review of the applications of biological records. *Biol. J. Linn. Soc.* 115, 532–542.
- Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., Isaac, N.J.B., 2019. Widespread losses of pollinating insects in Britain. *Nat. Commun.* 10, 1018.
- Pywell, R.F., Heard, M.S., Woodcock, B.A., Hinsley, S., Ridding, L., Nowakowski, M., Bullock, J.M., 2015. Wildlife-friendly farming increases crop yield: evidence for ecological intensification. *Proc. Biol. Sci.* 282.
- R Core Team, 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rader, R., Bartomeus, I., Tylianakis, J.M., Laliberté, E., 2014. The winners and losers of land use intensification: pollinator community disassembly is non-random and alters functional diversity. *Divers. Distrib.* 20, 908–917.
- Redhead, J.W., Sheail, J., Bullock, J.M., Ferreruela, A., Walker, K.J., Pywell, R.F., 2014. The natural regeneration of calcareous grassland at a landscape scale: 150 years of plant community re-assembly on Salisbury Plain, UK. *Appl. Veg. Sci.* 17, 408–418.
- Redhead, J., Fox, R., Brereton, T., Oliver, T., 2015. Assessing species' habitat associations from occurrence records, standardised monitoring data and expert opinion: a test with British butterflies. *Ecol. Indic.*
- Redhead, J.W., Woodcock, B.A., Pocock, M.J.O., Pywell, R.F., Vanbergen, A.J., Oliver, T. H., 2018. Potential landscape-scale pollinator networks across Great Britain: structure, stability and influence of agricultural land cover. *Ecol. Lett.* 21, 1821–1832.
- Redlich, S., Martin, E.A., Wende, B., Steffan-Dewenter, I., 2018. Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes. *PLoS One* 13, e0200438.
- Reidsma, P., Tekelenburg, T., Van den Berg, M., Alkemade, R., 2006. Impacts of land-use change on biodiversity: an assessment of agricultural biodiversity in the European Union. *Agric. Ecosyst. Environ.* 114, 86–102.
- Ribera, I., Dolédec, S., Downie, I.S., Foster, G.N., 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology* 82, 1112–1129.
- Ridding, L.E., Redhead, J.W., Pywell, R.F., 2015. Fate of semi-natural grassland in England between 1960 and 2013: a test of national conservation policy. *Global Ecol. Conserv.* 4, 516–525.
- Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* 39, 157–176.
- Robinson, E.L., Blyth, E., Clark, D.B., Comyn-Platt, E., Finch, J., Rudd, A.C., 2017. Climate Hydrology and Ecology Research Support System Meteorology Dataset for Great Britain (1961–2015). NERC Environmental Information Data Centre [CHESMet] v1.2.
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G., Ekbom, B., 2015. Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic Appl. Ecol.* 16, 250–259.
- Scherrer, D., D'Amen, M., Fernandes, R.F., Mateo, R.G., Guisan, A., 2018. How to best threshold and validate stacked species assemblages? Community optimisation might hold the answer. *Methods Ecol. Evol.* 9, 2155–2166.
- Schowalter, T.D., Noriega, J.A., Tschamtké, T., 2018. Insect effects on ecosystem services—Introduction. *Basic Appl. Ecol.* 26, 1–7.
- Senapathi, D., Carvalheiro, L.G., Biesmeijer, J.C., Dodson, C.-A., Evans, R.L., McKeerchar, M., Potts, S.G., 2015. The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. In: *Proceedings of the Royal Society B: Biological Sciences*, vol. 282.
- Sharp, R., Tallis, H.T., Ricketts, T., Guerry, A.D., Wood, S.A., Chaplin-Kramer, R., Bierbower, W., 2017. *INVEST 3.3.3 User's Guide*. The Natural Capital Project, Stanford.
- Sieling, K., Christen, O., 2015. Crop rotation effects on yield of oilseed rape, wheat and barley and residual effects on the subsequent wheat. *Arch. Agron Soil Sci.* 61, 1531–1549.
- Siram, C., Gross, N., Baillo, A.B., Bertrand, C., Carrié, R., Hass, A., Fahrig, L., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl. Acad. Sci. Unit. States Am.* 116, 16442–16447.
- Soil Survey of Scotland Staff, 1981. In: *Research, M.I.F.S. (Ed.), Land Capability for Agriculture Maps of Scotland at a Scale of 1:250 000*. Aberdeen.
- Stamp, L.D., 1931. The land utilization survey of Britain. *Geogr. J.* 78, 40–47.
- Swinbank, A., 2017. World trade rules and the policy options for British agriculture post-Brexit. Briefing paper 7, 12.
- Tenerelli, P., Carver, S., 2012. Multi-criteria, multi-objective and uncertainty analysis for agro-energy spatial modelling. *Appl. Geogr.* 32, 724–736.
- Tompkins, E.L., Few, R., Brown, K., 2008. Scenario-based stakeholder engagement: incorporating stakeholders preferences into coastal planning for climate change. *J. Environ. Manag.* 88, 1580–1592.
- Török, P., Deák, B., Vida, E., Valkó, O., Lengyel, S., Tóthmérész, B., 2010. Restoring grassland biodiversity: sowing low-diversity seed mixtures can lead to rapid favourable changes. *Biol. Conserv.* 143, 806–812.
- Walker, K.J., Stevens, P.A., Stevens, D.P., Mountford, J.O., Manchester, S.J., Pywell, R.F., 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biol. Conserv.* 119, 1–18.
- Welsh Government, 2017. *Predictive Agricultural Land Classification (ALC) Map*. The Land Quality Advice Service. Welsh Government, Llandrindod Wells.
- Williams, N.M., Crone, E.E., Roulston, T.A.H., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.* 143, 2280–2291.
- Winfrey, R., Fox, J.W., Williams, N.M., Reilly, J.R., Cariveau, D.P., 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.* 18, 626–635.
- Woodcock, B.A., Redhead, J., Vanbergen, A.J., Hulmes, L., Hulmes, S., Peyton, J., Heard, M.S., 2010. Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. *Agric. Ecosyst. Environ.* 139, 181–186.
- Woodcock, B.A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A.J., Heard, M.S., Pywell, R.F., 2014. National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. *J. Appl. Ecol.* 51, 142–151.
- Woodcock, B.A., Isaac, N.J., Bullock, J.M., Roy, D.B., Garthwaite, D.G., Crowe, A., Pywell, R.F., 2016. Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nat. Commun.* 7, 12459.
- Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J., Pywell, R.F., 2019. Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nat. Commun.* 10, 1481.
- Zhao, Z.-H., Hui, C., He, D.-H., Li, B.-L., 2015a. Effects of agricultural intensification on ability of natural enemies to control aphids. *Sci. Rep.* 5, 8024.
- Zhao, Z.-H., Sandhu, H.S., Gao, F., He, D.-H., 2015b. Shifts in natural enemy assemblages resulting from landscape simplification account for biocontrol loss in wheat fields. *Ecol. Res.* 30, 493–498.