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Does agri-environment scheme participation in England increase pollinator populations and crop pollination services?

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Abstract

Agri-environment schemes are programmes where landholders enter into voluntary agreements (typically with governments) to manage agricultural land for environmental protection and nature conservation objectives. Previous work at local scale has shown that these features can provide additional floral and nesting resources to support wild pollinators, which may indirectly increase floral visitation to nearby crops. However, the effect of entire schemes on this important ecosystem service has never previously been studied at national scale.

Focusing on four wild pollinator guilds (ground-nesting bumblebees, tree-nesting bumblebees, ground-nesting solitary bees, and cavity-nesting solitary bees), we used a state-of-the-art, process-based spatial model to examine the relationship between participation in agri-environment schemes across England during 2016 and the predicted abundances of these guilds and their visitation rates to four pollinator dependent crops (oilseed rape, field beans, orchard fruit and strawberries).

Our modelling predicts that significant increases in national populations of ground-nesting bumblebees and ground-nesting solitary bees have occurred in response to the schemes. Lack of significant population increases for other guilds likely reflects specialist nesting

resource requirements not well-catered for in schemes. We do not predict statistically significant increases in visitation to pollinator-dependent crops at national level as a result of scheme interventions but do predict some localised areas of significant increase in bumblebee visitation to crops flowering in late spring. Lack of any significant change in visitation to crops which flower outside this season is likely due to a combination of low provision of nesting resource relative to floral resource by scheme interventions and low overall participation in more intensively farmed landscapes.

We recommend future schemes place greater importance on nesting resource provision alongside floral resource provision, better cater for the needs of specialised species and promote more contiguous patches of semi-natural habitat to better support solitary bee visitation.

1 Introduction

Animal pollinators support reproduction in an estimated 87.5% of flowering plant species worldwide, including over three quarters of the world's leading food crops (Klein et al., 2007, Ollerton et al., 2011). In England, the most important pollinator-dependent crops are oilseed rape (*Brassica napus;* hereafter OSR), field beans (*Vicia faba*), orchard fruit (apples, pears, and plums) and soft fruit (mainly strawberries and raspberries) (Breeze et al., 2020; DEFRA, 2017). Pollination of these crops is mainly carried out by wild, unmanaged pollinators – principally bumblebees and solitary bees (Blitzer et al., 2016; Garratt et al., 2014a; Hutchinson et al., 2021; Klatt et al., 2013). There is evidence of widespread declines in wild bee populations in Great Britain between 1980 and 2013 (Powney et al., 2019), echoing a global trend of decline (IPBES, 2016). This can impact food security where floral visitation is insufficient to achieve optimal yield in pollinator-dependent crops (Garratt et al., 2014a; Holland et al., 2020). Even where this risk is not imminent, declining wild bee abundance and diversity can leave areas vulnerable to future shocks in bee populations or instability of other ecosystem services (Hutchinson et al., 2021; Senapathi et al., 2015).

Land use change, particularly the simplification of landscapes through intensified agriculture, is a major driver of pollinator decline (Ollerton et al., 2014; Potts et al., 2016) as the proportion of land used for crops and improved grassland increases at the expense of 'semi-natural habitat' such as hay meadows, fallow land, leys and hedgerows (Firbank et al., 2008; Ridding et al., 2020). Relative to crops and improved grassland, semi-natural habitat provides better quality nesting habitat (Lye et al., 2009) and provides floral resources on which pollinators can forage when managed crops are not in flower (Garratt et al., 2017; Kovács-Hostyánszki et al., 2017; Timberlake et al., 2019). Addressing wild bee declines and associated risks to ecosystem services therefore typically involves creating, restoring, or at least maintaining semi-natural habitat (Bommarco et al., 2013).

Agri-environment schemes (AES) are programmes where landholders enter into voluntary agreements (typically with governments) to manage agricultural land for environmental protection and nature conservation objectives (Dicks et al., 2016). In England, the main AES are *Countryside Stewardship* (CS) scheme (active since 2015) and the previous *Environmental Stewardship* (ES). In both schemes, landholders choose from a selection of over 200 multi-year management options and capital items with associated payment rates per option, based on costs and income forgone for loss of agricultural production.

Many options serve a broad environmental purpose aligned to the farming system such as hedgerow management, grass margins and low-input grassland. Others are specifically designed to restore or maintain habitats such as semi-natural grassland, moorland, and woodland, while capital items provide funding for one-off activities such as hedge planting. Where these options and items increase the quality and quantity of nesting and/or floral resources in a landscape, they can be valuable to pollinators depending on species' preferences (Vaudo et al., 2015). Some CS options have been explicitly designed to provide floral resources for wild bees and other pollinators in arable farms, (e.g. AB1 – Nectar flower mix, and AB16 – Autumn sown bumblebird mix) and its 'Wild Pollinator and Farm Wildlife Package' encourages farmers to bundle these with options that may provide nesting resources (e.g. hedgerows and field corner management).

Several studies demonstrate that these AES features can boost wild bee species richness and abundance at field and farm scale (Balfour et al., 2015; Heard et al., 2012; Scheper et al., 2015). The relationship between AES and crop pollination services is more complex and less well understood. A relationship between provision of AES features in agricultural landscapes and crop pollination services has been demonstrated empirically at farm and field scale (Blaauw and Isaacs, 2014; Morandin et al., 2016; Nicholson et al., 2017; Pywell et al., 2015), but, due to different bees foraging ranges and preferences (Kennedy et al., 2013) this is not consistent across feature type (Albrecht et al., 2020).

However, AES feature effectiveness at local scale does not necessarily translate into whole-scheme effectiveness at national scale. Schemes are not mandatory and even where farmers do participate, the choice of options implemented may not necessarily be the most effective at supporting wild bees due implementation cost influencing option choice (Austin et al., 2015). Since empirical approaches are unfeasible at national scale, detailed modelling that incorporates how bees move around the landscape to nest, forage and reproduce is needed to estimate the impact of AES on pollination service. The process-based pollinator model developed by Lonsdorf et al. (2009) and later developments of it (Häussler et al., 2017; Olsson et al., 2015) have this capability and have already been applied at regional scale to examine the impact of interventions (Cong et al., 2014; Davis et al., 2017; Häussler et al., 2017), while the latest state-of-the-art version (‘poll4pop’) has recently been validated in Great Britain for four wild bee guilds (Gardner et al., 2020).

This study integrates spatially explicit data from multiple sources to generate the most detailed and realistic map yet of AES, crop, and non-crop features across England for the year 2016. It then applies the fully validated poll4pop model to this landscape to predict wild bee abundance and the level of crop and non-crop pollination service provided. By comparing the pollinator model’s predictions including and excluding AES management, we estimate the schemes’ current effectiveness at promoting wild bee abundance and pollination services at national scale. The study provides an assessment of participation in schemes as a whole, including the effects of options that may not explicitly target pollinators but still have an effect through changing the quantity/quality of resources. Based on the findings, recommendations are made to increase the effectiveness and direct/incentivise participation in future AES.

2 Methodology

All modelling/data processing was carried out in ArcGIS 10.7 (ESRI, 2019) and Python 2.7 / 3.5. The Poll4pop model source code was transcribed from R (R Core Team, 2018) to Python to facilitate integration with ArcGIS and improve processing times.

2.1 Model Description

Poll4pop (Gardner et al., 2020; Häussler et al., 2017) is a process-based model that predicts seasonal spatially explicit abundance and floral visitation rates for central-place foraging pollinators in a given landscape including fine-scale features such as hedgerows and grass margins. It can be parameterised for a particular species or for a species grouping (‘guild’) with common attributes. A brief overview of the model is given as follows, but for a more detailed description see Häussler et al. (2017).

The model requires a land cover raster detailing the land class assigned to each cell as well as a rasterised map showing the area of 'edge' land classes (features smaller than the cell resolution – $25m^2$ in our case) within each cell. Each land class has a score representing the amount of floral resource provided during a given season (floral cover), the attractiveness of that floral resource to the guild (floral attractiveness; representing its nutritional quality), and its attractiveness as a nesting resource to that guild (nesting attractiveness). Floral cover and floral attractiveness are multiplied to generate a floral resource raster by season. The edge features are incorporated by taking the area-weighted sum of the edge and non-edge features in a given cell.

Nests are initially allocated to cells according to a Poisson distribution around the expected number per cell predicted from the nesting attractiveness raster and input maximum nest density. For every season during which the guild is active, foragers from each cell containing nests gather floral resources from cells within a distance-and floral-resource-weighted Gaussian kernel surrounding that cell. The size of the kernel is determined by a guild specific mean foraging distance parameter (β_f). The visitation rate to a given cell (per season) within the kernel is the product of its distance and floral resource weights. The total visitation rate to a given cell for that season (V_s) is the sum of all the visitation from all the nests whose kernels cover that cell.

For solitary guilds, the foragers are reproductive females, but for social guilds the reproductive females (queens) are replaced by foraging workers after the first season. For solitary guilds, the number of new reproductive females produced by a cell (Q) depends on the amount of resource gathered during the active period and a lognormal growth function with median, steepness, and maximum parameters specific to that guild. For social guilds, the number of workers produced by a cell (W_s) at the end of a season is determined by the amount of the resources gathered and a similar lognormal growth function specific to that guild. In the final active season for social guilds the resources are used to produce new reproductive females.

At the end of the final active season, new reproductive females disperse to cells within a distance- and nesting-attractiveness-weighted Gaussian kernel. The size of the kernel is determined by a guild specific mean nesting distance parameter (β_n). The number of nests in a given cell (R) in the following year is the sum of the nesting dispersal from all the kernels that cover that cell, subject to the maximum nest density parameter. The modelling process is repeated using these nests until the total number of nests in the landscape converges (<1% change between runs).

The model therefore outputs, per guild, three measures of abundance and a measure of visitation as rasters at the same resolution as the input rasters:

- Number of nests in a given cell (R).
- Number of workers produced at the end of a given season by the nests in a given cell and thus available to forage in the next season (W_s) – social bees only.
- Number of new reproductive females produced at the end of the final active season by the nests in a given cell (Q).
- Flower visitation rate in a cell for a given season (V_s).

We note that these predicted visitation rates do not include visitation by other non-modelled pollinators, that crop yield ultimately depends non-linearly on this visitation rate and that the relationship between our predicted visitation rates and the rate required for optimum pollination of any given crop is still uncertain (see Discussion). Nonetheless, by simulating foraging and population processes, the model represents the best tool currently available for assessing how fine-scale changes in habitat provision/configuration may influence bee abundance and visitation rates at landscape-scale.

2.2 Model Parameterisation and Validation

Gardner *et al.* (2020) - hereafter G2020 – parameterised and validated the poll4pop model in Great Britain for four guilds: ground-nesting bumblebees, ground-nesting solitary bees, tree-nesting bumblebees, and cavity-nesting solitary bees. We took guild specific parameters for foraging and dispersal distance, population growth and maximum nest density directly from G2020 and Häussler *et al.* (2017).

G2020 used 33 land classes and derived their (guild-specific) floral attractiveness and nesting attractiveness parameters and floral cover parameters across three seasons (spring, summer, autumn) via an expert opinion survey (Table S7-11 in Supplementary Material.). We adopt their values and derive additional attractiveness and floral cover parameters for our extended range of land cover as described in section 2.3.2 below.

We also readjust the seasonal definitions for floral cover to represent early spring (early/mid-March – late April/early May), late spring (late April/early May - early/mid-June) and summer (early/mid-June - early/mid-August) to better capture differences in flowering windows for mass-flowering arable crops (generally late spring flowering) and orchards (generally early spring flowering) relative to floral resources created by AES features (flowering across spring). Our early and late spring floral cover parameters relate to the original spring G2020 parameters as follows:

- OSR, Linseed/flax, Peas, Field beans, Strawberries/raspberries not in polytunnels, Other berries: the G2020 floral cover parameter for spring was allocated 90% to late spring and 10% to early spring.

- Orchards: the G2020 floral cover parameter was allocated 90% to early spring and 10% floral to late spring.
- All other land classes: the G2020 floral cover parameter was allocated 50% to early spring and 50% to late spring.

The 90/10 allocation was used rather than 100/0 since late spring flowering crops will have some inflorescence in Early Spring (see e.g. AHDB (2020) for OSR), whilst some orchard cultivars flower into late spring.

We repeated the validation process carried out by G2020 to confirm that our extended parameter set, and new seasonal definitions still produce model predictions that agree with observed pollinator abundances (see Supplementary Material – Section 5).

2.3 AES Present and AES Absent Scenarios

In order to make predictions for pollinator abundances and visitation rates with, and in the absence of, current AES management, we generated land cover and edge input rasters at 25m^2 resolution for two scenarios: '*AES_Present*' representing the scenario where the AES management was present, and '*AES_Absent*' representing the scenario where AES management was absent. The year 2016 was chosen because it was the most recent to have agricultural, non-agricultural and AES spatial data at sufficient resolution. A brief overview of the process is given in the following section, with a detailed description provided in the Supplementary Material.

2.3.1 Source landcover data

Land cover and edge feature information were sourced to represent as closely as possible the coverage of non-agricultural land, crops and permanent grassland, and land under agri-environment scheme (AES) option management for England during the year 2016. We included a 5km buffer zone into Scotland and Wales to eliminate edge effects based on the largest mean dispersal distance parameter (1km for bumblebee nesting).

Agricultural land cover for England came from 2016 Basic Payment Scheme (BPS) claims data identifying the type and area of crop, grassland or other eligible feature and was assigned to the corresponding polygon from the Land Parcel Information System (LPIS). Orchard polygons were sourced from the Ordnance Survey Master Map Orchards layer (MMOrch; Ordnance Survey, 2017).

Land outside LPIS and MMOrch was classified according to land cover information from the CEH Landcover Map 2015 (LCM; Rowland *et al.*, 2017). Two additional data sources - Crop Map of England 2016 (CROME; Rural Payments Agency, 2019) and OpenStreetMap (OSM; OpenStreetMap contributors, 2017) - were used to determine land class where there was inconsistency between the LCM, LPIS and BPS datasets: i.e. where LCM indicated 'Arable or Horticulture' but there was no corresponding LPIS polygon, or where there was a LPIS polygon with no corresponding BPS claim (see Supplementary Material Section 2 for more detail.)

Two English AES schemes had active agreements during 2016: the current Countryside Stewardship (CS) scheme (open since 2015) and Environmental Stewardship (ES), the legacy scheme open to applications prior to 2015. We sourced AES features from both schemes' datasets (CS: Natural England, 2018; ES: Natural England, 2018) selecting only options with agreements active during 2016. Features that would not impact on habitat quality for bees (e.g. water troughs, archaeological site management) or whose management impact was outside the seasonal scope of the model (e.g. winter cover actions) were removed. A full list of excluded options is provided in the Supplementary Material (Table S5).

ES and CS datasets only provide a LPIS reference and the length or area of feature. So, we implemented a process to split up LPIS parcel polygons into smaller components representing the individual AES features and the remainder of the parcel (See Supplementary Material Section 2.3). Where the AES option type was too small to be resolved at $25m^2$ cell resolution in the subsequent raster conversion, we used an analogous process to create polylines (e.g. at the polygon boundary) appropriate to the option.

Buffer strips and hedgerow features in BPS claims relate to Environmental Focus Areas (EFA) under Common Agricultural Policy ‘Greening’ requirements (Rural Payments Agency, 2018). These were assumed equivalent to the simplest buffer strip creation and hedgerow maintenance options in ES and were converted to appropriate length polylines at the parcel boundary, avoiding duplication with equivalent AES features. Other hedgerow features were created from the CEH Woody Linear Features Framework (WLF; Scholefield et al., 2016) and a woodland edge polyline layer was created at the boundaries of contiguous LCM woodland features.

2.3.2 Parameterising changes in land cover habitat quality

Our combined source data included 28 non-agricultural land cover types, 128 agricultural land cover types and 364 AES land cover types. Below we detail how we align these with the 33 land classes already parameterised by G2020 for use in the poll4pop model and how intermediate parameters are derived where required to represent the more subtle changes generated by AES management. Full details are in the Supplementary Material Section 1.

Land in AES was assigned an *AES_Present* land class and an AES_Absent land class with reference to Defra Reports BD2302 (University of Hertfordshire, 2009) as refined in BD5007 (University of Hertfordshire, 2011); – hereafter, BD2302/5007). These reports describe the expected land cover resulting from the option (used to generate *AES_Present*) and the absence of management (used to generated *AES_Absent*). Assignment of *AES_Present* and *AES_Absent* land classes to CS options was made using an 'Equivalency Table' provided by Natural England (the scheme developer) that links these options to their ES equivalents (Natural England, 2018 *pers. comm*). Option descriptions provided in scheme manuals (Natural England, 2013; 2015) were used where required.

For some options, the descriptions in both the *AES_Present* and *AES_Absent* scenarios could be matched directly to G2020 land classes. For example, land under the CS option LH3 (Creation of heathland from arable or improved grassland) was mapped to "Moorland" in *AES_Present* and an arable crop type or improved grassland in *AES_Absent* as appropriate. These options received the attractiveness and floral cover scores for those land classes in each respective scenario. For other options, the G2020 land classes were not sufficient to match the description given in one or both of the scenarios. G2020 only has land classes for intensively managed land (agricultural crops, improved grassland / meadow) or broad habitats (unimproved grassland / meadow, moorland, wetland, woodland) while the BD2302/5007 descriptions reflect more subtle transitions in land cover. To capture these distinctions, new land classes (e.g. semi-improved grassland, degraded moorland, etc.) were created by blending existing G2020 land classes to approximate the description given in BD2302/BD5007. The attractiveness and floral cover parameters for these blended land classes were set to the weighted average of the parameters from their constituent G2020 land classes. When hedgerows, ditches and woodland edges are not in AES, they are assumed to still be present with the same associated parameter values, but their width is halved in the *AES_Absent* scenario to model the reduced management.

Land not in AES was assigned the same land cover class as G2020 with the exception of semi-natural grassland categories in LCM (acid grassland, neutral grassland, calcareous grassland) which were assigned to a semi-improved grassland category rather than an unimproved grassland category as per the LCM metadata (CEH, 2017). As this land was outside AES in both scenarios, the classification was the same in *AES_Present* and *AES_Absent*. The final parameter values used for all land classes, the weighting rules for new land classes, and the guild-specific parameters are shown in the Supplementary Material (Table S1).

2.3.3 Assessment of change in abundance and visitation rates

The model was run to generate abundance and visitation rate predictions for each guild in each season for the *AES_Present* and *AES_Absent* scenarios, respectively. For solitary bees (active during only one season) we simulated spring-flying and summer-flying populations separately, where spring-flying populations used the cumulative resources from both Early and Late Spring.

The change in predicted visitation rate V for season s (V_s) due to the presence of AES management at cell level was assessed by calculating the log ratio between the predicted visitation rates in the two scenarios ($log_{10}(V_{s\_AES\_Present}/V_{s\_\_AES\_Absent})$. The ratios are logged to ensure that reductions in visitation rate have the same magnitude as proportionally equivalent increases. Cells with identical visitation rates in both scenarios will therefore have a value of 0, while +1 represents a tenfold increase in visitation rate in the presence of AES features and -1 a tenfold decrease. The same log ratio approach was applied to calculate the predicted change in new reproductive production (Q), new nest production (R), and new worker production per season (W_s).

To estimate the uncertainty in the log ratio caused by uncertainty in the underlying parameter values, 100 simulations were run where the nesting attractiveness, floral attractiveness and floral cover score for each land class were drawn from a beta distribution ($B(a, b)$) with mean ($\mu = a / (a + b)$) and variance ($\sigma^2 = \mu(1 - \mu) / (a + b + 1)$)

equal to the mean and variance of the G2020 expert opinion scores for that parameter. A beta distribution was used as the scores are bounded and, since *B(a, b)* is only defined on the interval (0,1), the randomly drawn scores are rescaled to the appropriate scale for that parameter. For new blended land classes, where the mean value was generated by averaging the scores of two existing classes, the variances were calculated using error propagation (Hughes and Hase, 2010). Draws for land classes were constrained as described in the Supplementary Material to prevent instances that unreasonably exceeded the range of expert opinion.

The significance of the change in visitation rate with respect to the uncertainty in underlying habitat quality parameters was assessed by calculating the standard deviation of the 100 simulations of the log ratio visitation rate and then measuring how many standard deviations a given cell or region's log ratio visitation rate was from the no change value of zero (the point at which the ratio would be 1:1). A log ratio more than 2 standard deviations away from zero was considered to show a significant change in visitation rate between *AES_Present* and *AES_Absent* scenarios. Locations where the log ratio was more than 3 standard deviations from zero were considered a highly significant difference.

To examine the overall impact at national scale on different land resources such as pollinator-dependent crops and semi-natural habitat, the land classes are grouped into categories (Table 1). Detail of individual land class allocations to these categories is given in Table S1 (Supplementary Material). The total impact of AES participation and its significance on a particular land category at national level is calculated for the log ratio of the sum of V_s, Q, R, and W_s across all cells in England within that category for *AES_Present* and *AES_Absent* respectively.

Table 1: Land Categories

Land Category	**Description**

Oilseed Rape (OSR)	Pollinator-dependent crop
Field Beans	Pollinator-dependent crop
Strawberries	Pollinator-dependent crop; includes all open-grown strawberries (i.e., excluding those grown in polytunnels) and Raspberries
Orchards	Pollinator-dependent crop
Other Crops	Any other crop not listed above
Improved Grassland	
Semi-natural Habitat	This covers all land that is not a classified as crop, improved grassland, suburban or urban. It therefore includes hedgerows, ditches, grass/flower margins, fallow areas, grass/legume leys, semi-natural grassland, moorland, heathland, wetland, woodland, and coastal habitats.
Suburban	Suburban areas (areas with a mixture of buildings and gardens), parks
Urban	Built-up areas with little vegetation, e.g. city centres & industrial estates, Also includes other null value land cover such as open water and rock
All Land	All land classes listed above

2.4 Exemplar Area

To illustrate the fine-scale effects predicted by our 25m^2 resolution simulations at farm-scale, we selected an exemplar area in western England to present alongside the national maps. This area was chosen because it is one of the few areas in England to grow all four pollinator-dependent crops and it represents a heterogeneous landscape incorporating a variety of agri-environment interventions.

3 Results

3.1 Area and distribution of crops and land under AES

The pollinator-dependent crops OSR (621,014 ha) and field beans (189,332 ha) were grown across much of lowland England during 2016, while orchard fruit (39,335 ha) and strawberries (2,914 ha) were concentrated in certain areas of south-east and western England (Figure 1a; Figure S13a-b; Figure S14a-b). Otherwise, England's agricultural area was dominated by other crops (not pollinator-dependent) and improved grassland. There was over 3.5M ha of semi-natural habitat of potential value to wild bees including hedgerows, ditches, grass/flower margins, heathland, and woodland. ~1.5M ha of this was under AES management (Figure S15a) but the rest was outside the CS and ES schemes (Figure S15b). Suburban parks and gardens (highly valuable pollinator habitat) covered ~1.0M ha.

Only 108,237 ha (~7% of the AES area) involved the creation of semi-natural habitat at the expense of crops or improved grassland (Figure 1b). The remaining area comprised options that aim to maintain, restore, or enhance *pre-existing* semi-natural habitat. AES participation rates and type of option applied are also linked to land use intensity. Much of the upland area (generally farmed extensively) was in AES and there were many field-scale features. In arable regions (generally farmed intensively) the participation rates were lower, mostly consisting of linear features with some small and dispersed field-scale options. Participation rates were lower in the orchard fruit and strawberry growing areas relative to areas where only OSR and field beans were cultivated (compare exemplar area patterns in c, d of Figure S13, Figure S14 and Figure S15).

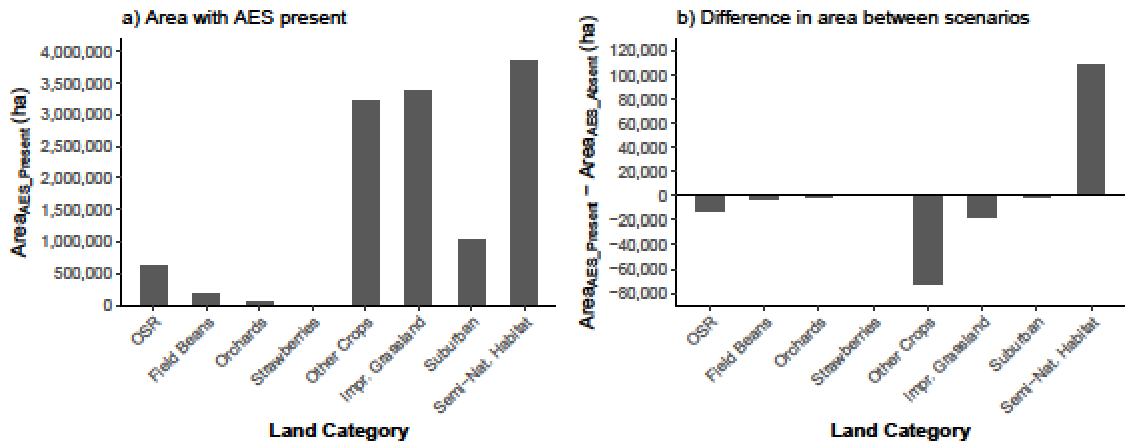

Figure. 1 a) Total area by land category in England for 2016 when Agri-environment scheme (AES) features are present - AES_Present scenario; b) Area change (ha) between scenarios with AES feature present (AES_Present) and absent (AES_Absent). in each land category. The Urban land category is excluded as it is parameterised with no resource value.

3.2 Impact of AES participation on pollinator abundance at national level

Nest productivity (number of new reproductive females produced per cell) is predicted to be significantly higher for ground-nesting guilds when AES management is present (Figure 2 – ‘All land’) with relative increases of 10.4% for ground-nesting bumblebees and 15.4% / 7.8% for spring-active / summer-active ground-nesting solitary bees.

Nest density is also predicted to be significantly higher for ground-nesting guilds when AES management is present (Figure 3, ‘All land’) with increases of 4.6% for ground-nesting bumblebees and 16.2% for spring-active ground-nesting solitary bees. The predicted increase in nest density for summer-active ground-nesting solitary bees is not significant. Semi-natural habitat shows the largest and consistently significant nest density increases (6.6% and 36.9% for the above-mentioned guilds respectively) across the land categories and this drives the change in the ‘All land’ category. Significant nest density increases in crop and improved grassland categories for ground-nesting solitary bees are relatively small (2.8% – 9.0%) while no significant overall increase is predicted for tree-nesting bumblebees or cavity-nesting solitary bees (Figures S4, S5 in Supplementary Material).

AES management is also predicted to have a significant overall positive impact on ground-nesting bumblebee worker production in late spring (increase of 8.15%; Figure 4b ‘All Land’) although semi-natural habitat is the only land category to show a significant increase (11.5% equivalent). Overall increases in worker production are predicted for early spring but these are not significant given current uncertainties, the exception being a small but significant predicted increase in the worker population for nests in orchards during early spring (2.5% equivalent). No significant overall change in tree-nesting bumblebee worker production is predicted, though the results do show a similar significant increase for orchards in early spring (Figure S3 in Supplementary Material.).

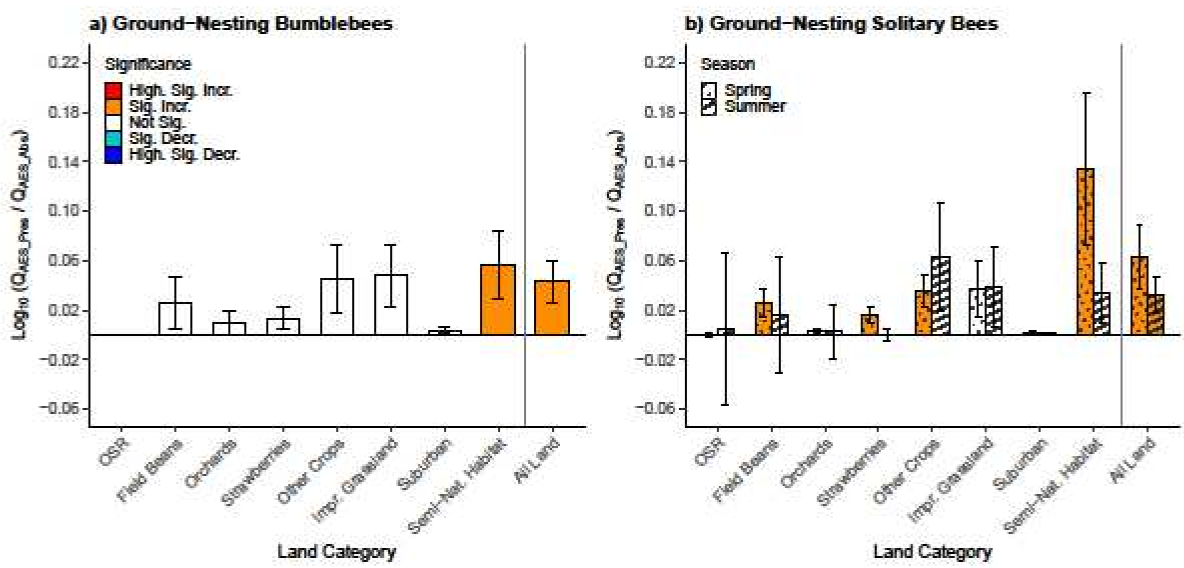

Figure 2. Predicted impact of Agri-environment schemes (AES) on nest productivity (Q; production of new reproductive females per 25 m2) nationally to all land categories and subdivided by land category for (a) ground-nesting bumblebees and b) ground-nesting solitary bees (separated by active season). The impact is measured as the log of the ratio between the scenarios with AES features present and absent. Significance thresholds are number of standard deviations that the log ratio is above (increase) or below (decrease) zero: value > =|3| is highly significant, |2| < = value < |3| is significant. See Supplementary Material for other guilds.

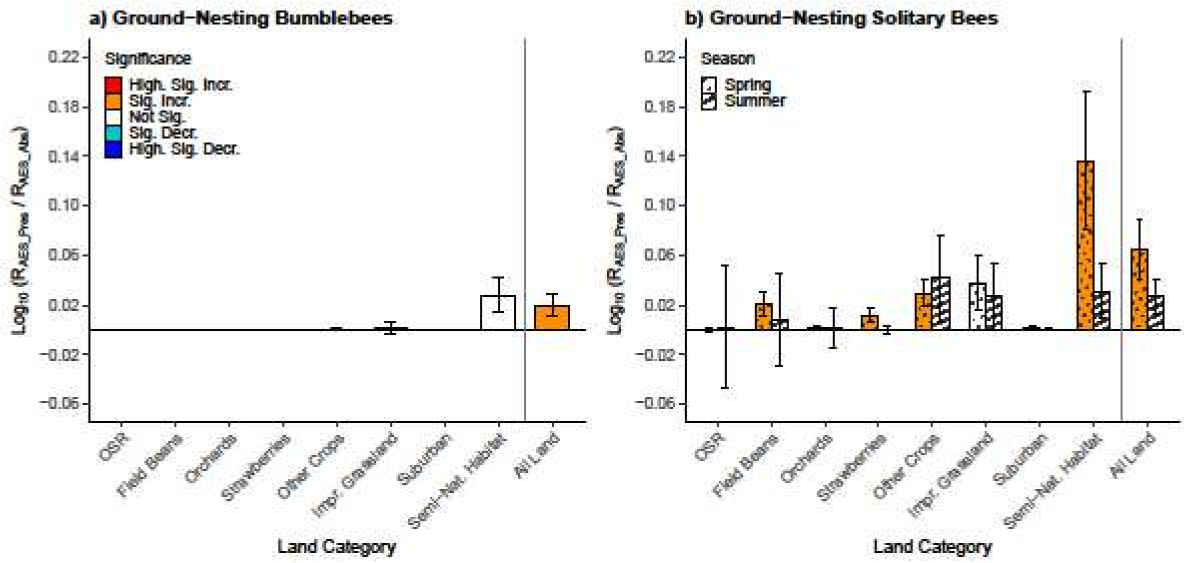

Figure 3. Predicted impact of Agri-environment schemes (AES) on nest density (R; nests per 25 m2 cell) nationally to all land classes and subdivided by land category for (a) ground-nesting bumblebees and b) ground-nesting solitary bees (separated by active season). The impact is measured as the log of the ratio between the scenarios with AES features present and absent. Significance thresholds are number of standard deviations that the log ratio is above (increase) or below (decrease) zero: value > =|3| is highly significant, |2| < = value < |3| is significant. See Supplementary Material for other guilds.

3.3 Impact of AES participation on floral visitation rate at national level

The model predicts significantly higher floral visitation overall (across all land categories) in Early Spring and Summer for ground-nesting bumblebees (+4.6% and +8.2% respectively; Figure 5) and in Early and Late Spring for ground-nesting solitary bees (+16.2% both seasons). Visitation to semi-natural habitat is also predicted to be significantly higher for these guilds in those seasons. Predicted increases for tree-nesting bumblebees and cavity-nesting solitary bees are not significant overall or for semi-natural habitat (see Figure S4 in the Supplementary Material).

Although the model predicts increased visitation rate to OSR and field beans during peak flowering (Late Spring) due to AES management, this increase is only significant for the case of ground-nesting solitary bees to field beans where visitation rises by 6.2% (Figure 5). An increase of similar scale and significance to field beans is also predicted for cavity-nesting solitary bees. The absolute change in both cases is not large and is from a low base (e.g. V_s in *AES_Absent* for field beans is 0.19 for ground-nesting solitary bees compared to 7.9 for ground-nesting bumblebees; Figure S9 in the Supplementary Material).

There are no significant changes to orchard or strawberry visitation at national-level, with the exception of tree-nesting bumblebees where the model predicts a small but significant decrease in visitation in Early Spring (-2.2%; Figure S4, Supplementary Material). Tree-nesting bumblebees are also predicted to show reduced visitation to OSR, Field Beans in Early Spring (-4.5% in both cases) in the presence of AES features. This is not a flowering season for these crops, so the change is relative to a very low absolute visitation rate (V_s in *AES_Absent* is 0.12 and 0.03 for OSR and field beans, respectively).

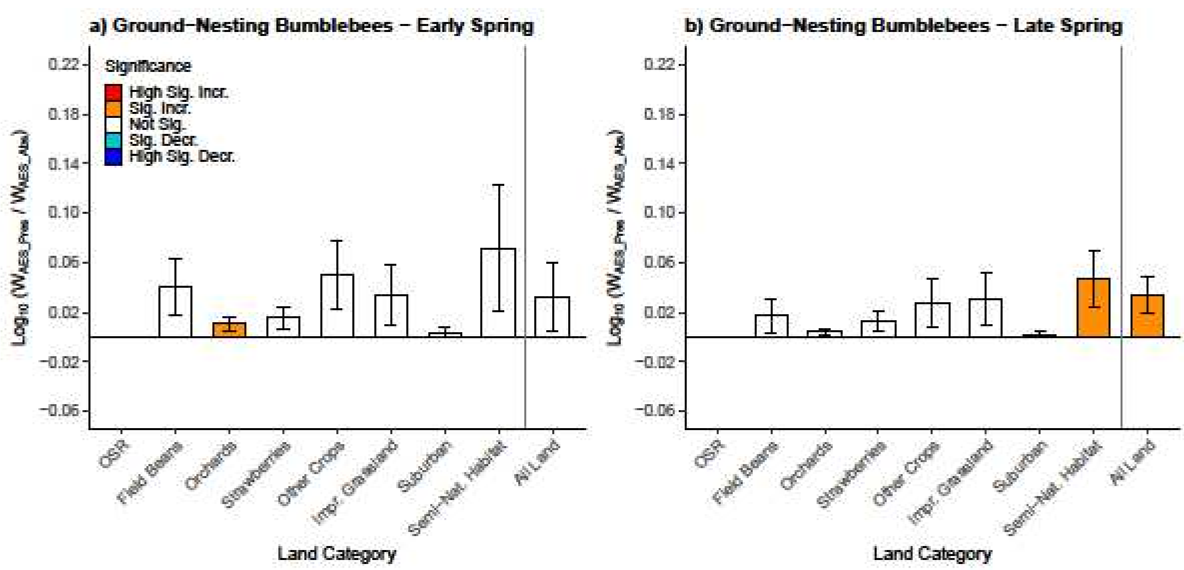

Figure 4. Predicted impact of Agri-environment schemes on ground-nesting bumblebee worker production (W; workers produced per 25 m2 cell) nationally to all land classes and subdivided by land category for (a) Early Spring and (b) Late Spring. The impact is measured as the log ratio between the scenarios with AES feature present and absent. Significance thresholds are number of standard deviations that the log ratio is above (increase) or below (decrease) zero: value > =|3| is highly significant, |2| < = value <|3| is significant. Early spring: early/mid-March – late April/early May. Late spring: late April/early May - early/mid-June. See Supplementary material for tree-nesting bumblebees.

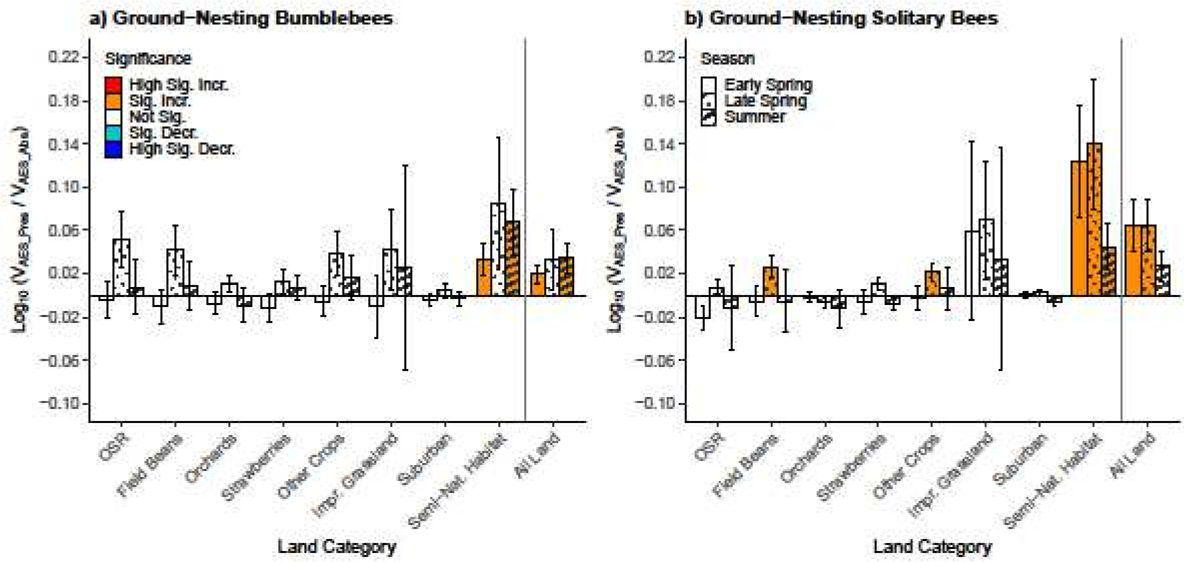

Figure 5. Predicted impact of Agri-environment schemes (AES) on floral visitation rate (V; visits per 25 m2 cell) nationally to all land classes and subdivided by land category for (a) ground-nesting bumblebees and b) ground-nesting solitary bees in each season. The impact is measured as the log ratio between the scenarios with AES feature present and absent. Significance thresholds are number of standard deviations that the log ratio is above (increase) or below (decrease) zero: value > =|3| is highly significant, |2| < = value < |3| is significant. Early spring: early/mid-March – late April/early May. Late spring: late April/early May - early/ mid-June. Summer: early/mid-June – early/mid-September. See Supplementary Material for other guilds.

3.4 Impact of AES participation on floral visitation rate at cell-level

Despite a lack of significant changes at national-level, Figure 7 shows that significant increases are predicted in localised areas for both ground-nesting guilds in late spring. Closer inspection of their distribution within the exemplar area (Figure 7c-d) shows significant increases occurring for cells which correspond to AES management locations. There are also localised areas of significant increase covering a defined neighbourhood around these locations, whose extent is related to bee foraging range. These neighbourhoods are typically narrow for solitary bees (approx. 250-500m radius) and are usually isolated, whilst the neighbourhoods of significant bumblebee visitation increase extend to a wider radius (approx. 1-2km) and often merge with each other. The scale of increase in late spring is generally 0.1 to 2-fold in the neighbourhood and 2 to 10-fold within the AES cells. The effect is less evident in other seasons (see Figure 6 for early spring and Figure S16 in the Supplementary Material for summer).

The presence of a neighbourhood effect has implications for crop pollination services where pollinator-dependent crops form part of this neighbourhood. 46.4% of the national OSR cropping area and 36.1% of the national field bean cropping area is predicted to experience a significant or highly significant increase in ground-nesting bumblebee visitation during what is the peak flowering season for these crops (Figure 8c). 11.5% of the orchard resource is also predicted to benefit from increased late spring ground-nesting bumblebee visitation but this will only be beneficial if those orchards are growing late flowering cultivars. 20% of strawberry cells also experience a significant or highly significant ground-nesting bumblebee visitation increase in Late Spring.

By contrast less than 5% of the resource for any of the pollinator-dependent crops are predicted to receive significantly increased ground-nesting solitary bee visitation during this season (Figure 8d). There is very little neighbourhood effect for pollinator-dependent crops in Early Spring (Figure 8a, b). This is peak flowering season for orchard fruit and only 0.9% and 2.3% of orchard cells are predicted to experience a significant or highly significant increase for ground-nesting bumblebee and ground-nesting solitary bee visitation. Likewise, very few cells are predicted to receive significantly more bee visitation in Summer (Figure S16, Supplementary Material).

Tree-nesting bumblebees show similar trends to the ground-nesting bumblebees, although fewer cells are predicted to receive significantly more visitation (for OSR and Field Beans in Late Spring those proportions are 26.1% and 20.3%, respectively; Figure S11, Supplementary Material), while the percentage of cropland with significant changes in cavity-nesting solitary bees visitation is similar to that for ground-nesting solitary bees.

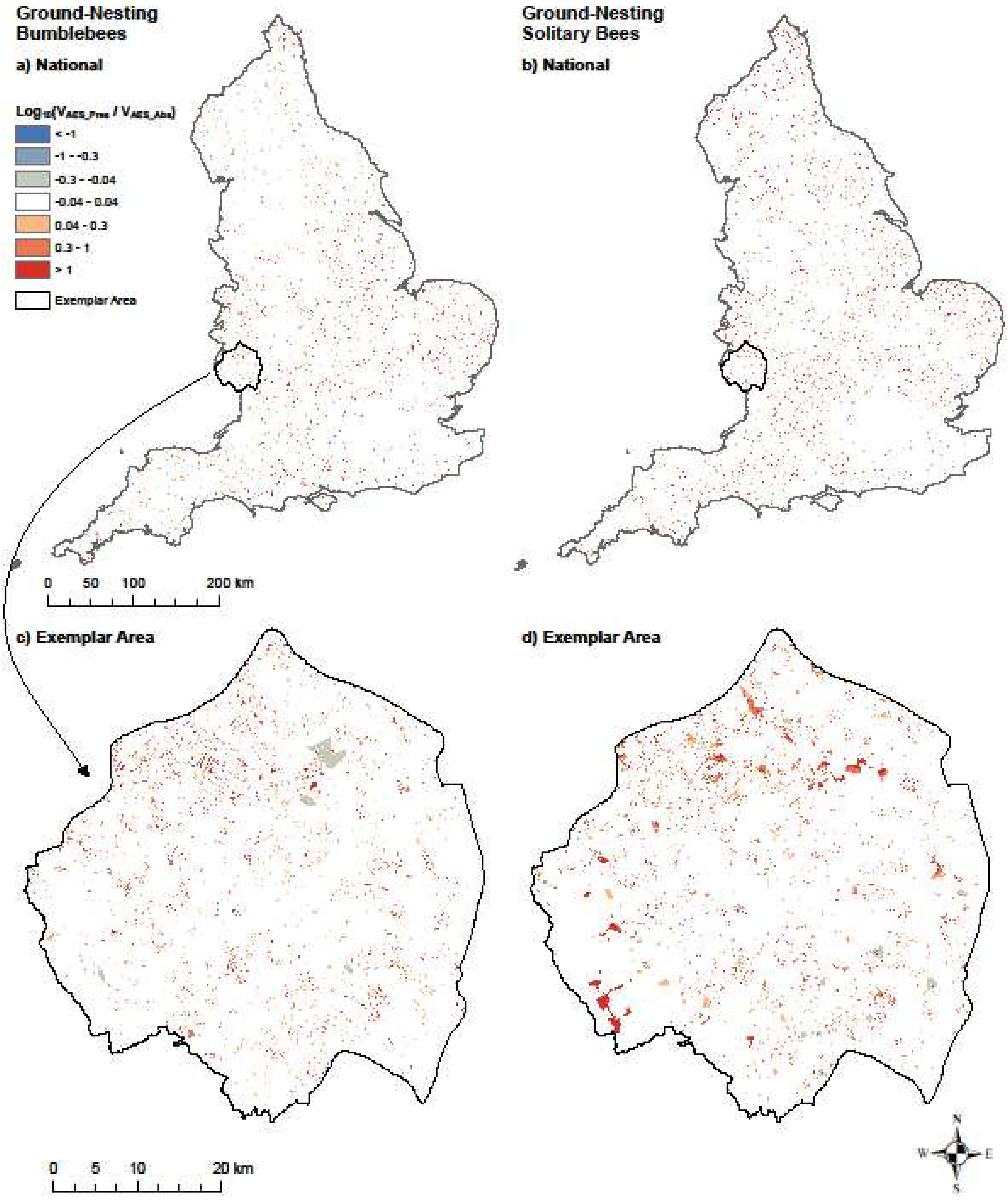

Figure 6. Impact of Agri-environment schemes on floral visitation rate (V) for ground-nesting guilds in England for early spring 2016 at cell-level nationally (a, b) and within an exemplar area (c, d) in western England. The impact is shown as the log of the ratio of V (visitation/25 m2) between the scenarios with AES feature present and absent. Only cells with significant change are shown - where the log ratio is at least 2 standard deviations from zero. Early spring: early/mid-March – late April/early May. See Supplementary material for other guilds.

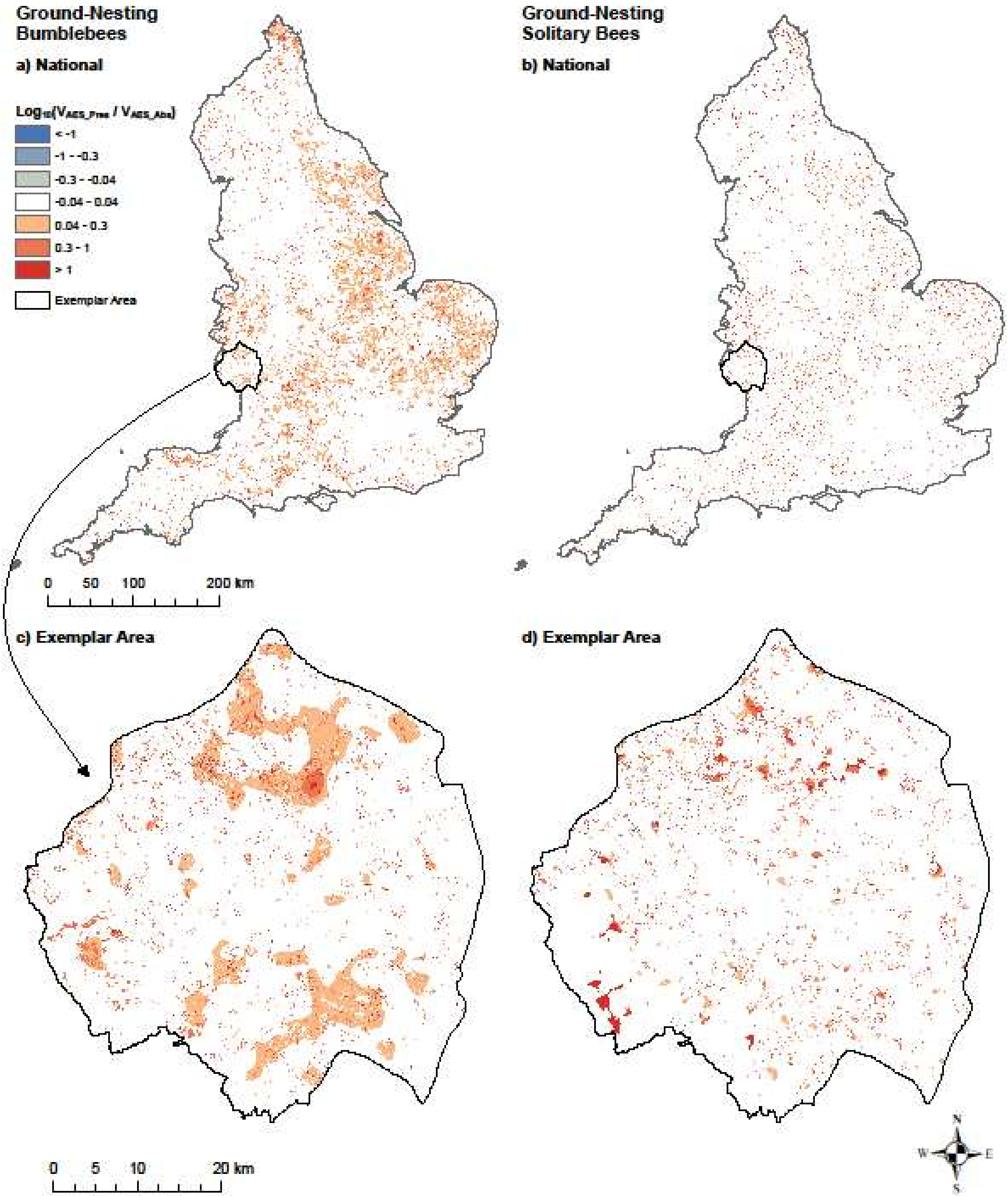

Figure 7. impact of Agri-environment schemes on floral visitation rate (V) for ground-nesting guilds for late spring 2016 at cell-level nationally (a, b) and within an exemplar area (c, d) in western England. The impact is shown as the log of the ratio of V (visitation/25 m2) between the scenarios with AES feature present and absent. Only cells with significant change are shown - where the log ratio is at least 2 standard deviations from zero. Late spring: late April/early May - early/mid-June. See Supplementary Material for other guilds.

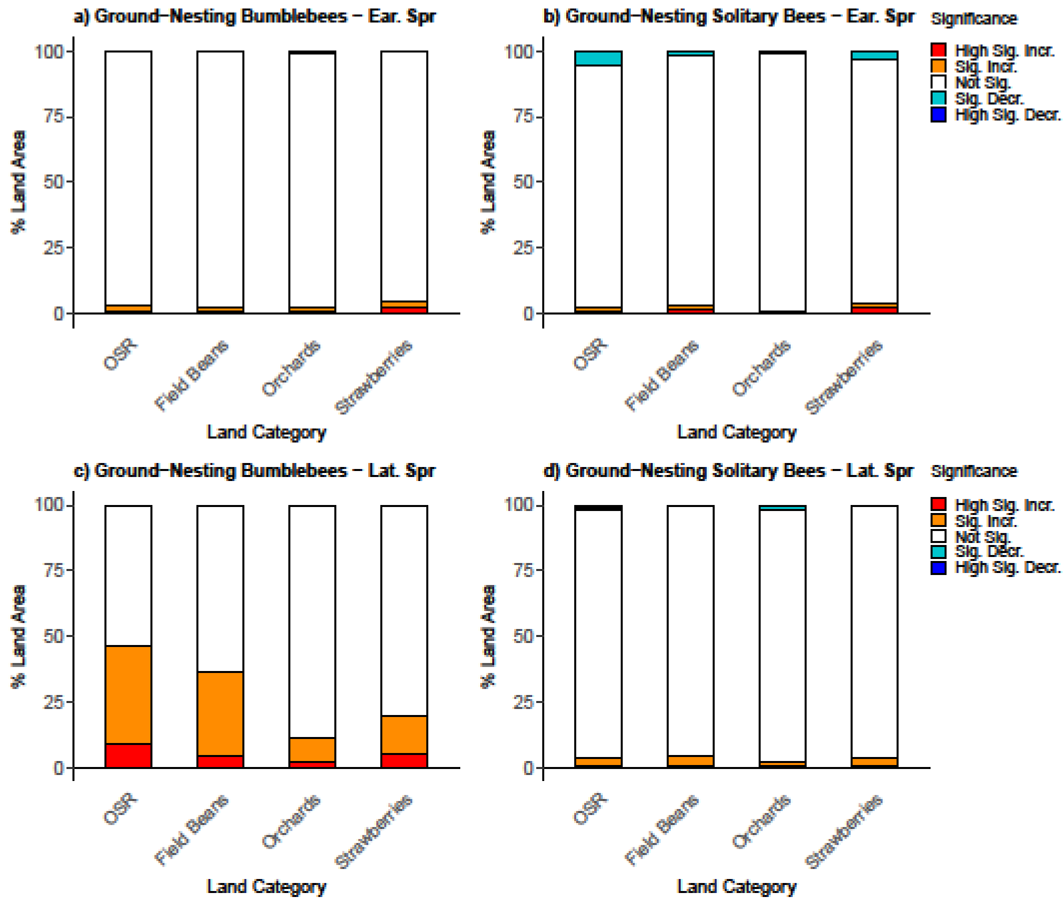

Figure 8. Percentage of cropland area within significance thresholds for predicted impact of Agri-environment schemes (AES) on floral visitation rate (V; visits per 25 m2 cell) for ground-nesting guilds in early (a, b) and late (c, d) spring. The impact is measured as the log ratio between the scenarios with AES feature present and absent. Significance thresholds are number of standard deviations that the log ratio is above (increase) or below (decrease) zero: value > =|3| is highly significant, |2| < = value < |3| is significant. Early spring: early/mid-March - late April/early May; Late spring: late April/early May - early/mid-June. See Supplementary material for other guilds.

4 Discussion

This study applied a validated spatially explicit process-based model (poll4pop) to examine changes in pollinator abundance and pollination service provision due to uptake of agri-environment scheme (AES) options across the whole of England for the year 2016. The model was used to compare bee visitation rates across four guilds in a scenario where the agri-environment features and/or management were present (*AES_Present*) with an alternative scenario where these were absent (*AES_Absent*).

The predictions suggest that participation in AES increased bee abundances, but these increases were only significant nationally for ground-nesting guilds. No significant increase is predicted for tree-nesting bumblebee and cavity-nesting solitary bee populations. We also predict significantly increased floral visitation rates nationally by ground-nesting guilds but only consistently within the semi-natural habitat enhanced by AES management. On average, visitation to pollinator dependent crops did not significantly increase nationally, but our simulations suggest some significant localised increases in visitation to late-spring flowering crops (predominantly OSR and field beans) by bumblebees. We do not predict enhanced crop visitation in other seasons from any guild.

4.1 Impact of AES on pollinator abundance

Predicted significant increases in nest productivity, nest density, and the number of workers for ground nesting guilds align with results of fieldwork in England demonstrating a significant relationship between observed bee abundances and presence of AES management (Crowther and Gilbert, 2020; Wood et al., 2015). The lack of predicted significant increases in the national-level abundance outputs for tree-nesting bumblebees or cavity-nesting solitary bees may be because few AES options provide or increase the quality of their preferred nesting habitat (Crowther et al., 2014; Gresty et al., 2018), as reflected in the expert opinion parameters assigned to these guilds for key AES options (e.g., flower rich margins, semi-improved/unimproved grassland, fallow, hedgerow – see Table S13 in Supplementary Material). The greater benefits of AES to spring-active, rather than summer active, ground nesting solitary bees is likely due to the early season boost in floral resources when there is less alternative floral provision from land outside schemes (Scheper et al., 2015).

Interestingly, our modelling suggests that the significant increases in nest productivity for ground-nesting bumblebees, induced by AES participation, are not matched by significant increases in nest density. This suggests the increased foraging resources provided by AES participation support larger pollinator populations during the active season, but this is not being met with a corresponding increase in the availability of nesting resources for new queens. AES schemes have focused on boosting bee abundances through floral resource provision (Dicks et al., 2015), however our predictions suggest schemes should pay increased attention to nesting resource availability (Requier and Leonhardt, 2020).

Predicted increases in abundance (number of new reproductive females) are predominantly associated with semi-natural habitats, which are typically of higher floral and nesting quality under AES participation. We do also predict an increase in solitary bee nest abundance in some crop fields (Figure 2b, Figure S2b), although abundance in these areas still remains low compared to semi-natural habitats (Figure S6b, d). The experts who provided the model's habitat scores assigned some limited solitary bee nesting value to certain crop types (Tables S9, S10), assumed to represent nesting opportunities in bare but untilled margins/tramlines, etc. The predicted increase in in-crop nests therefore likely reflects the fact that solitary bee reproductive females produced within adjacent AES features face limited availability of their preferred nesting habitat, due to their limited dispersal range (βn = 100m vs 1000m for bumblebees) and the relatively low semi-natural habitat coverage in arable areas (Figure S15).

4.2 Impact of AES on pollination services

The simulations predict significant and often large (2 to 10-fold) increases in visitation at cells under AES management (where floral and nesting values have generally increased relative to their value in *AES_Absent*). There is also a significant but generally smaller "neighbourhood effect" representing 0.1 to 2-fold changes in predicted visitation to surrounding cells outside AES management, where resource value is otherwise unchanged. The magnitude and direction of this neighbourhood effect depends on the guild and season. Where foraging is done by reproductive females (i.e. solitary bees in all seasons and bumblebees in early spring), increased neighbourhood visitation only occurs if the nesting density has increased sufficiently to offset the relative increase in floral value within the AES cell (Zamorano et al., 2020). Otherwise, there will be no change or even potentially sink effects where foragers are drawn away from neighbouring cells (see Figure S17 for tree-nesting bumblebees in early spring). For bumblebees in later seasons, workers do the foraging so floral resource increases support higher worker production rates and thus higher neighbourhood foraging rates without the need for increases in nest density (Riedinger et al., 2014).

The neighbourhood effect extends over a larger area for ground-nesting bumblebees compared to ground-nesting solitary bees due to their larger foraging and dispersal ranges (β_f = 530m vs 191m; β_n = 1000m vs 100m). This enables bumblebee populations to forage and disperse more widely, especially in more fragmented landscapes (Cranmer et al., 2012), so extending their neighbourhood effect. To encourage more solitary bee visitation into crops, schemes would need to provide larger, contiguous habitat features that better account for their limited dispersal range (Martínez-Núñez et al., 2020; Woodcock et al., 2013). In so doing, schemes would also help increase the diversity of pollinators provided thus increasing the resilience of the service.

A contributing factor towards the lack of a significant change in national visitation from ground-nesting bumblebees in late spring (despite significant changes in other seasons) could be the much larger variance in predictions for this guild for this season. This is driven by high uncertainty in the change in floral resource value for the 14,830 ha of semi-natural habitat in *AES_Present* where AES features have replaced (late-spring-flowering) OSR or field beans in *AES_Absent* (Figure 1).

4.2.1 Effect on OSR and field beans

At national scale, 46% of OSR and 36% of field bean area receive increased visitation from ground nesting bumblebees (key pollinators of both crops; Hutchinson et al. (2021)) due to the presence of AES. Flowering OSR and field beans are attractive resources relative to the surrounding landscape (Kovács-Hostyánszki et al., 2013), so additional bees supported by AES are then attracted to this resource. Even a small increase in semi-natural habitat area due to AES can increase populations which would otherwise be constrained by the relatively low floral quality of mass-flowering crops at other times of the year (Holzschuh et al., 2016; Riedinger et al., 2015). In areas where OSR and field bean visitation is not predicted to increase, this may reflect insufficient cover or placement of higher quality AES in general (Krimmer et al., 2019), uptake of AES land classes with higher resource parameter uncertainty (e.g. semi-natural grassland), or nesting limitation (see above) which can constrain the scale of the neighbourhood effect.

AES are predicted to have less impact on mass-flowering crop visitation by solitary bees. Only field beans, where solitary bees are not a common pollinator (Garratt et al., 2014b; Hutchinson et al., 2021; Nayak et al., 2015) show any significant change. This is again due to the shorter foraging and dispersal ranges of solitary bees, with much of the increased visitation stemming from greater nesting within the field bean cells themselves and the apparently substantial fractional change simply due to the very low level of solitary bee visitation predicted to this crop in both scenarios. By contrast, OSR is an attractive floral resource to solitary bees (Knopper et al., 2016), but to promote increased visitation by these guilds, AES management would need to be better distributed to enable these short-range foragers to reach a greater proportion of the crop.

4.2.2 Effect on orchard fruit and strawberries

At national scale, there was no significant increase in visitation to orchard or strawberry cells due to AES during their peak flowering seasons (early spring and summer, respectively). Both crops are predominantly located in areas of England that have relatively low AES participation (Figure S14, S15). Field studies elsewhere in Europe have found significantly lower populations of wild bees in the vicinity of commercial orchards (Eeraerts et al., 2017; Marini et al., 2012). This was attributed to lack of habitat diversity, suggesting that greater targeting of AES towards orchards would be beneficial for visitation, especially in more intensive agricultural landscapes (Holzschuh et al., 2012). Landscape fragmentation and simplification around strawberry crops is also associated with lower wild bee abundance and lower crop visitation rates (Bukovinszky et al. 2017; Castle et al., 2019; Connelly et al., 2015).

However, when wildflower strips have been experimentally introduced to orchards, no significant impact on pollination service is observed (Campbell et al., 2017; McKerchar et al., 2020). Placing wildflower strips alongside strawberries can increase visitation to the crop (Feltham et al., 2015), though the visitation is not always consistent across the field (Ganser et al., 2018). Meanwhile, manually increasing the population of bees through *in situ* nest provision does increase pollination of both crops (Bosch et al., 2006; Horth and Campbell, 2018).

Early spring orchard visitation is dependent on reproductive females, and we do not predict nest density increases in orchards (Figure 3). Although workers are available to forage on strawberry crops, their peak flowering season (summer) coincides with that of many AES interventions, potentially causing competition for pollinators. Significant increases in visitation to both these crops will therefore only be achieved if AES provide a large increase in nest density (which increases the absolute number of foragers) relative to the increase in floral value provided (which decreases the relative attractiveness of the crop). Scheme design may also need to change to increase the financial incentive available to fruit growers as current AES payment rates may not cover the income foregone in more productive agricultural areas where these crops are grown (Lastra-Bravo et al., 2015).

4.3 Caveats

Although the poll4pop model is sophisticated, it currently has limited temporal resolution (three seasons) and does not allow for mortality during ‘hunger gaps’ at the start/end of the active period (Jachuła et al., 2021). Some AES hedgerow options may provide floral resources in early-March (due to tree/shrub flowering) and again in autumn via flowering ivy (*Hedera helix*), while options promoting legume and herb-rich swards may also provide important late resources such as red clover (*Trifolium pratense*). Wild bees in English landscapes are highly dependent on these resources at these critical points for survival of reproductive females (Timberlake et al., 2019). We may therefore have underestimated the value of some AES options due to the relatively coarse temporal resolution of our model.

Our application of the model generalised wild bees into four guilds, but this may overstate the value of AES to bee species. For ground-nesting solitary bees in particular, field data suggests AES only provide beneficial floral resources for a minority of common species (Wood et al., 2017). We also note that an increase in visitation rate for one guild alone does not necessarily mean an increase in pollination service if the level of pollination service in the absence of the intervention is already sufficient to achieve optimal pollination, less pollinator-dependent crop varieties are grown or there are other limiting factors (Garratt et al., 2018). Further work is needed to link model visitation rates to yield in order to examine the impact of schemes on pollination service deficits.

Our study has sought to predict the extent to which participation in AES at scheme level, given current uptake patterns, has changed wild bee guild abundances and flower visitation rates. The geographic variation in magnitude and significance of the effect will depend on the type, quantity, quality (relative resource value-add) and placement of the AES resource with respect to crops or other areas of interest. The relative importance of these factors and the relative importance of individual interventions in driving these predicted scheme-level changes will be investigated in forthcoming work.

5 Conclusions and Recommendations for Policy

This study has demonstrated how a sophisticated process-based model (poll4pop) can be used in conjunction with detailed landcover data to examine the effectiveness of entire agri-environment schemes (AES) at supporting bee populations and the ecosystem services they provide. Our results also demonstrate the potential of this approach to inform selection and targeting of AES incentives to enhance these outcomes.

Our modelling predicts that the pattern of AES participation in 2016 was effective in boosting ground-nesting bee populations compared to a scenario without these features. However, tree-nesting and cavity-nesting bee populations nationally were not predicted to benefit from AES participation. Furthermore, current AES participation was not predicted to significantly increase visitation to pollinator-dependent crops at national level. Significant localised increases were predicted only for late-spring flowering crops (OSR and field beans), and these were delivered by bumblebees. Motivated by our predictions we summarise below our recommendations for future AES design in England:

- **Floral resource provision**. Our predictions for ground-nesting bee populations align with monitoring data suggesting a slowing of the decline in recent years for generalist bee species due to AES (Powney et al., 2019) and with estimates that a 2% land allocation to floral cover options within AES would provide sufficient resource for common wild bee species (Dicks et al., 2015). Schemes should therefore continue to incentivise floral resource provision.

- **Nesting resource provision**. We identified nest site limitation as preventing populations from fully benefiting from the increased floral resource provided by AES features and as a contributing factor in our prediction for lack of significant national increase in crop visitation. Schemes should enhance the uptake and sophistication of options that provide nesting resources, especially in orchard- and strawberry-growing regions. Interspersing larger, more contiguous patches of semi-natural habitat within arable areas may also better support short-range solitary bee populations and their pollination services.
- **Resource diversity**. Tree-nesting and cavity nesting bee species have habitat requirements that are not well-catered for in current AES. To increase populations of these guilds, schemes should increase the range of interventions that provide specialist nesting and floral resources. Although more bespoke and locally specific features may be required to support some species, AES could support these guilds generically through options that create/manage hedgerows, trees, and scrub (in potentially good alignment with current carbon sequestration goals that also favour such options; Summers et al. (2021)).

6 Author contributions

MI conceived the ideas, carried out the research and wrote the manuscript. TB and EG contributed to conceptual development and manuscript revisions. YC and EG provided the poll4pop model and parameters which MI adapted and applied to this context. All other authors provided comments on the manuscript and/or datasets for model validation.

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