

Which interventions contribute most to the net effect of England's agri-environment schemes on pollination services?

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Published Version

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Image, M., Gardner, E., Clough, Y., Kunin, W. E., Potts, S. G. ORCID: <https://orcid.org/0000-0002-2045-980X>, Smith, H. G., Stone, G. N., Westbury, D. B. and Breeze, T. D. ORCID: <https://orcid.org/0000-0002-8929-8354> (2023) Which interventions contribute most to the net effect of England's agri-environment schemes on pollination services? *Landscape Ecology*, 38. pp. 271-291. ISSN 1572-9761 doi: 10.1007/s10980-022-01559-w Available at <https://centaur.reading.ac.uk/109102/>

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To link to this article DOI: <http://dx.doi.org/10.1007/s10980-022-01559-w>

Publisher: Springer

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Which interventions contribute most to the net effect of England's agri-environment schemes on pollination services?

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Received: 13 March 2022 / Accepted: 10 November 2022
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Abstract

Context Agri-environment schemes support land management interventions that benefit biodiversity, environmental objectives, and other public goods. Process-based model simulations suggest the English scheme, as implemented in 2016, increased wild bee pollination services to pollinator-dependent crops and non-crop areas in a geographically heterogeneous manner.

Objectives We investigated which interventions drove the scheme-wide predicted pollination service increase to oilseed rape, field beans and non-cropped areas. We determined whether the relative contribution of each intervention was related to floral and/or nesting resource quality of the intervention, area of uptake, or placement in the landscape.

Methods We categorised interventions into functional groups and used linear regression to determine the relationship between predicted visitation rate increase and each category's area within a 10 km grid tile. We compared the magnitude of the regression coefficients to measures of resource quality, area of uptake nationally, and placement to infer the factors underpinning this relationship.

Results Hedgerow/woodland edge management had the largest positive effect on pollination service change, due to high resource quality. Fallow areas were also strong drivers, despite lower resource quality, implying effective placement. Floral margins had limited benefit due to later resource phenology. Interventions had stronger effects where there was less pre-existing semi-natural habitat.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-022-01559-w>.

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Conclusions Future schemes could support greater and more resilient pollination service in arable landscapes by promoting hedgerow/woodland edge management and fallow interventions. Including early-flowering species and increasing uptake would improve the effect of floral margins. Spatial targeting of interventions should consider landscape context and pairing complimentary interventions to maximise whole-scheme effectiveness.

Keywords Pollination services · Agri-environment schemes · Bees · Semi-natural habitat · Interventions

Introduction

Agri-environment schemes (AES) provide economic support to landholders who enter into voluntary agreements (typically with governments) to manage land to benefit biodiversity, meet environmental objectives and deliver other public goods (Dicks et al. 2016). Many schemes allow landholders to choose from a set of interventions based on suitability for the farming system, geographical context and the type of habitats already present on the farm. Current schemes in England offer a variety of interventions in the form of ‘management options’ that support the creation, restoration and/or management of habitat features such as hedgerows, field margins, fallow areas, flower-rich leys, low-input grassland, as well as semi-natural grassland, moorland, wetland, and woodland (Natural England 2013, 2018a). Agri-environmental schemes therefore reduce the amount of land being intensively managed and increase the quality and quantity of semi-natural habitat.

Wild bees (bumblebees and solitary bees) significantly contribute to pollination and thus yield of oilseed rape (*Brassica napus*; hereafter OSR) and field beans (*Vicia faba*) (Hutchinson et al. 2021), two economically important UK arable crops. Wild bees’ population sizes are limited by access to forage resources (Roulston and Goodell 2011) and also by nest site availability (Steffan-Dewenter and Schiele 2008; Carrié et al. 2018). Objectives for AES interventions are not necessarily wild bee-specific, but many of them can provide important non-crop floral and nesting resources for wild bees, thus increasing individual reproductive output and overall population sizes. This has been demonstrated empirically

for specific AES interventions including floral margins (Carvell et al., 2015), hedgerows (Timberlake et al. 2019) and grassland management (Berg et al. 2019), as well as for AES interventions more generally (Crowther and Gilbert 2020). Field and farm scale analyses have shown that by increasing populations of wild bees, AES can indirectly contribute to increased crop visitation (Pywell et al. 2015; Morandin et al. 2016). Moreover, by supporting pollination of wild flowers AES also contribute to wider integrity of ecosystem-level pollination services (Senapathi et al. 2015).

Understanding the impacts of agri-environment schemes on wild bee abundance and pollination service at larger spatial scales requires modelling that reflects how bees (central place foragers) move in the landscape to nest, forage and reproduce. The process based model poll4pop (Häussler et al. 2017; Gardner et al. 2020) has this capability, by building on earlier attempts to capture landscape complementarity and foraging movements (Lonsdorf et al. 2009; Olsson et al. 2015). Image et al. (2022) (hereafter IM2022) used poll4pop to predict the national scale impact of 2016 AES participation on wild bee abundances and visitation rates to different land cover types in England. The model predicted that AES participation led to nationally significant increases in ground-nesting bumblebee and ground-nesting solitary bee abundances, and significant increases in visitation to non-crop plants. However, only 46% of the national OSR cropping area and 36% of the national field bean cropping area were predicted to experience significantly increased ground-nesting bumblebee visitation. For both crops, increases in ground-nesting solitary bee visitation were predicted for less than 5% of crop areas.

Although comprehensive, IM2022 only captured the effect of all AES interventions collectively. In practice, schemes are offered as sets of interventions where participants have flexibility as to the type, quantity and location of interventions implemented. Individual interventions differ in their floral and/or nesting value contributions (Cole et al. 2020) but the effect of an individual intervention depends on its placement relative to pollinator-dependent crops as well as its quantity and quality (Albrecht et al. 2020). The change in visitation achieved may also potentially depend on the interaction between intervention types: for example, one intervention that individually

provides only good nesting resource, and a second intervention that provides only a good floral resource may be more effective if co-located. The effect on pollination service may also be dependent on the quantity of pre-existing floral and/or nesting resource: if this is already high then the baseline pollination service may also be high so that the marginal effect of AES interventions will be low (Tscharntke et al. 2005). Examining how different types of intervention have contributed to the overall predicted change in the context of their quality, quantity and placement could help to understand the uneven pattern of pollination service enhancement and inform which interventions or combinations to promote in future schemes.

Here, we grouped > 350 individual AES options into categories according to habitat type and extent of land-use change and used regression analysis to determine the contribution of each group to the overall increase in visitation rate to OSR, field beans and non-cropped areas predicted by IM2022. A regression approach is used rather than repeating the IM2022 method for individual groups because it allows us to account for the interaction between different AES intervention groups and with existing semi-natural habitat. We then consider how intervention quality, quantity, and placement in the landscape influence these effects, enabling recommendations to be made for how future AES could better support pollination services.

Methods

Predicted change in visitation due to AES

Estimates of the predicted change in wild bee visitation in England due to AES participation were obtained from IM2022. We briefly outline below how these predictions were subsequently processed for use in the current study.

Pollinator model description

IM2022 used the process-based model poll4pop (Häussler et al. 2017; Gardner et al. 2020), which predicts seasonal spatially-explicit abundance and floral visitation rates for central-place foraging pollinators within a given rasterised landscape, incorporating fine-scale features such as hedgerows and

grass margins. The model simulates optimal foraging of bees around their nests and population growth to calculate within-year production of workers for social bees and yearly population size for all bees (see IM2022 for an overview and Häussler et al. (2017) for a detailed description) and can be run for a particular species or for a group of species ('guild') that have common attributes. The model requires: a land cover map, floral cover parameters for each land cover class in each season, floral and nesting attractiveness (i.e. foraging and nesting quality to the modelled species or guild) for each land cover class, maximum nest density and mean foraging and dispersal range for the species/guild, and a set of parameters determining nest productivity in terms of how many new (workers and) reproductive individuals are produced as a function of forage resources gathered.

The model was run for four wild bee guilds (ground-nesting bumblebees, ground-nesting solitary bees, tree-nesting bumblebees, and cavity-nesting solitary bees) taking guild-specific parameters from Gardner et al. (2020). These parameters consisted of literature estimates, plus nesting and floral attractiveness and floral cover scores derived from expert opinion, which IM2022 augmented to allow for additional land classes and to incorporate seasonal adjustments related to crop flowering. Finally, the model was validated against observed bee abundance to demonstrate that model parameters correctly reproduced observed abundance trends across a range of landscapes. Full details of the parameterisation and validation are provided in IM2022.

AES feature mapping

IM2022 simulated two landcover scenarios for England in the year 2016: one in which AES supported management was present (*AES_Present*) and an alternative in which AES supported management was absent (*AES_Absent*). The English AES schemes included were *Countryside Stewardship* (CS) and *Environmental Stewardship* (ES), though field margin and hedgerow features claimed by landholders as Ecological Focus Areas (EFA) under Common Agricultural Policy 'Greening' requirements (Rural Payments Agency 2018) were also treated as AES. Locations of AES features were obtained from UK Rural Payments' Agency datasets and land cover maps (at 25 m resolution) for the two scenarios were

developed as set out in IM2022. Allocation of AES management options to land cover classes in *AES_Present* and *AES_Absent* was made with reference to Defra Reports BD2302 (University of Hertfordshire 2009), BD5007 (University of Hertfordshire 2011) or intervention descriptions (Natural England 2018a, b).

Calculating change in visitation due to AES

IM2022 predicted floral visitation rates for each guild for three seasons: 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) under both scenarios for every 25 m cell in England. In the present study, we aggregated these past results to 10 km level (Ordnance Survey tiles) to allow an efficient scale for further analysis; this scale is large enough for bee population dynamics within the tile to dominate over exchange of bees with surrounding tiles (bumblebee have the largest foraging and dispersal ranges in the model, being 530 m and 1 km, respectively) whilst still being small enough to capture geographic differences in crop and AES intervention type coverage.

We identified the OSR cells (see Figs. 1, 2 for their location) and took the 25 m cell-level floral visitation (by guild) predictions to those cells during late spring, when OSR is pollinated. We then aggregated these values to the 10 km tile level and divided by the number of cells to generate the average visitation rate. Where cells contained edge features, the crop visitation rate was adjusted *pro rata* to the proportion of crop resource and its floral resource value (floral attractiveness * floral cover) relative to the edge features. The visitation rate for the *AES_Present* scenario was divided by the visitation rate for the *AES_Absent* scenario to generate the visitation ratio (Fig. 2a) which was the dependent variable reflecting the change in visitation to OSR. We did the same calculation for field beans (Figs. 1b, 2b), again for late spring when beans are pollinated. A similar process was followed for non-cropped land cover, but the visitation rates were summed across all three seasons (Figs. 1c, 2c). Non-cropped land included all semi-natural habitat, improved grassland (including grass leys), and suburban parks/gardens. As with IM2022, for each tile we also calculated uncertainty by running 100 simulations where nesting attractiveness, floral attractiveness and floral cover score for each

land class were drawn from a beta distribution, representing the variation in individual expert opinion scores for these parameters, to generate a standard deviation for the visitation ratio at 10 km tile level (see Supplementary Material).

Although we ran the analyses for all four wild bee guilds, here we have focused on ground-nesting bumblebees as this was the only guild showing a widespread and significant response in OSR and field bean visitation rates due to AES management in IM2022. Results for the other three guilds are provided in the Supplementary Material.

Classification of AES into categories

The IM2022 dataset contained 364 distinct AES management options (interventions) derived from CS, ES and EFA datasets. Each had an effect on floral and nesting resource quality, determined by the change in its land class allocation (and associated parameterisation) in the *AES_Present* and *AES_Absent* scenarios. We grouped management options into ten categories (Table 1) based on the type of habitat feature and management objective (category allocations of all 364 interventions are shown in Supplementary Table S1). This removed redundancy and collinearity where several interventions had identical or similar qualitative effects and were likely to be taken up in similar geographies. Considering broad categories rather than specific interventions also made the results more transferable and generalisable to future schemes and other countries.

The quantity of each AES category varied geographically (Fig. 3a–j). The categories also exhibited different changes in nesting and floral resource quality change with respect to the *AES_Absent* scenario (Fig. 4). Field margin options requiring landholders to sow with flowers (floral margin) had greater floral attractiveness than those which are sown with grasses only (grass margins), but the latter provided more attractive nesting habitat (Fig. 4; Table S1). We also separated interventions that change land use from crops or improved grassland to semi-natural habitat (creation) from those that maintain or restore existing semi-natural habitat (habitat management), as the latter typically imply a smaller change in resources in our parameterisation (Fig. 4). We grouped grassland and heathland creation into a common category as overall resource change is similar for our guild-level

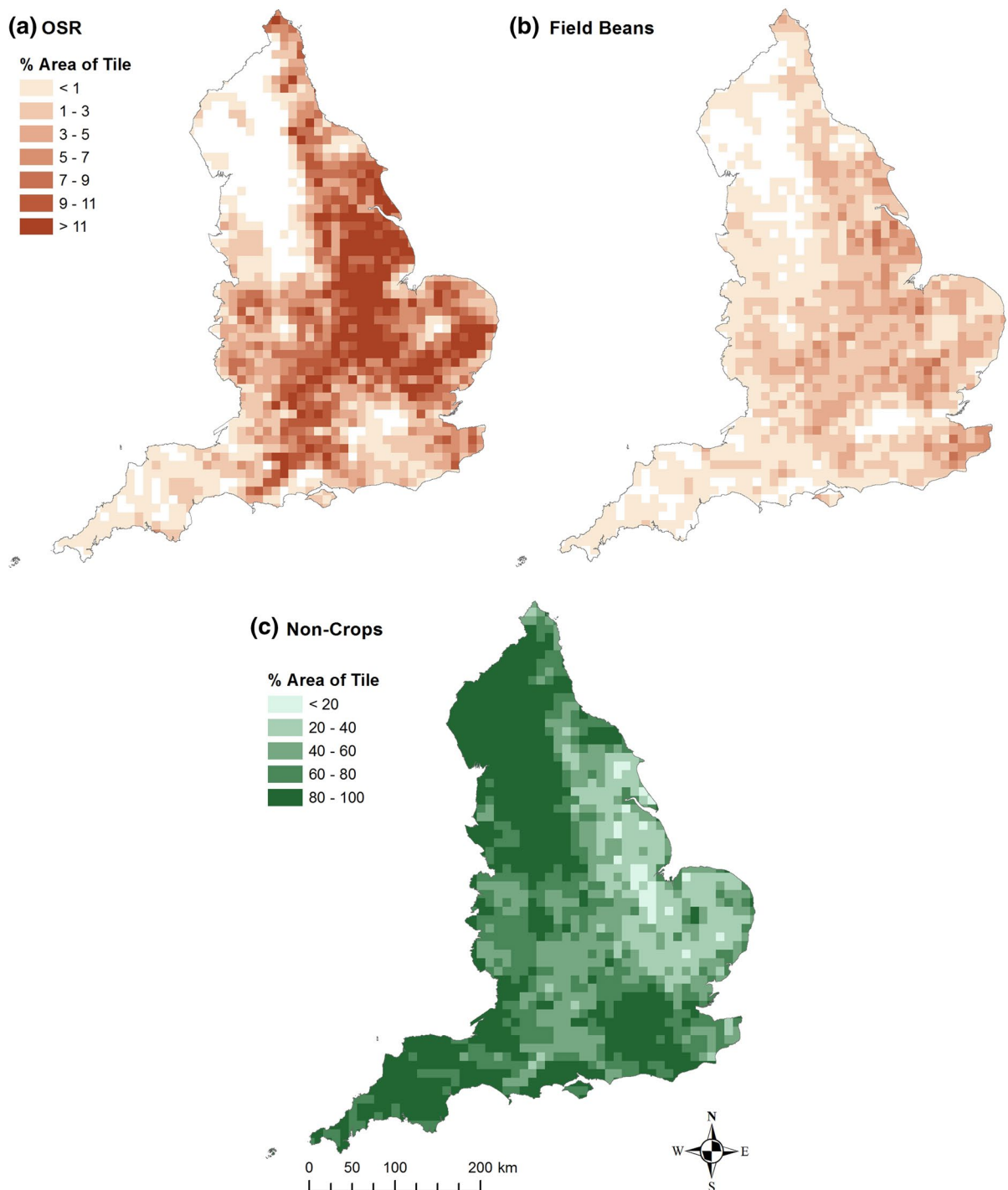


Fig. 1 Coverage of **a** OSR, **b** Field Beans and **c** Non-Crop land cover by 10 km tile for England in 2016. Non-crop means all land classes that are not arable crops

analysis. Likewise, we grouped woody linear feature management (hedgerows, woodland edge) into a

single category, but we separated traditional orchards from other tree creation options (scrub, woodland,

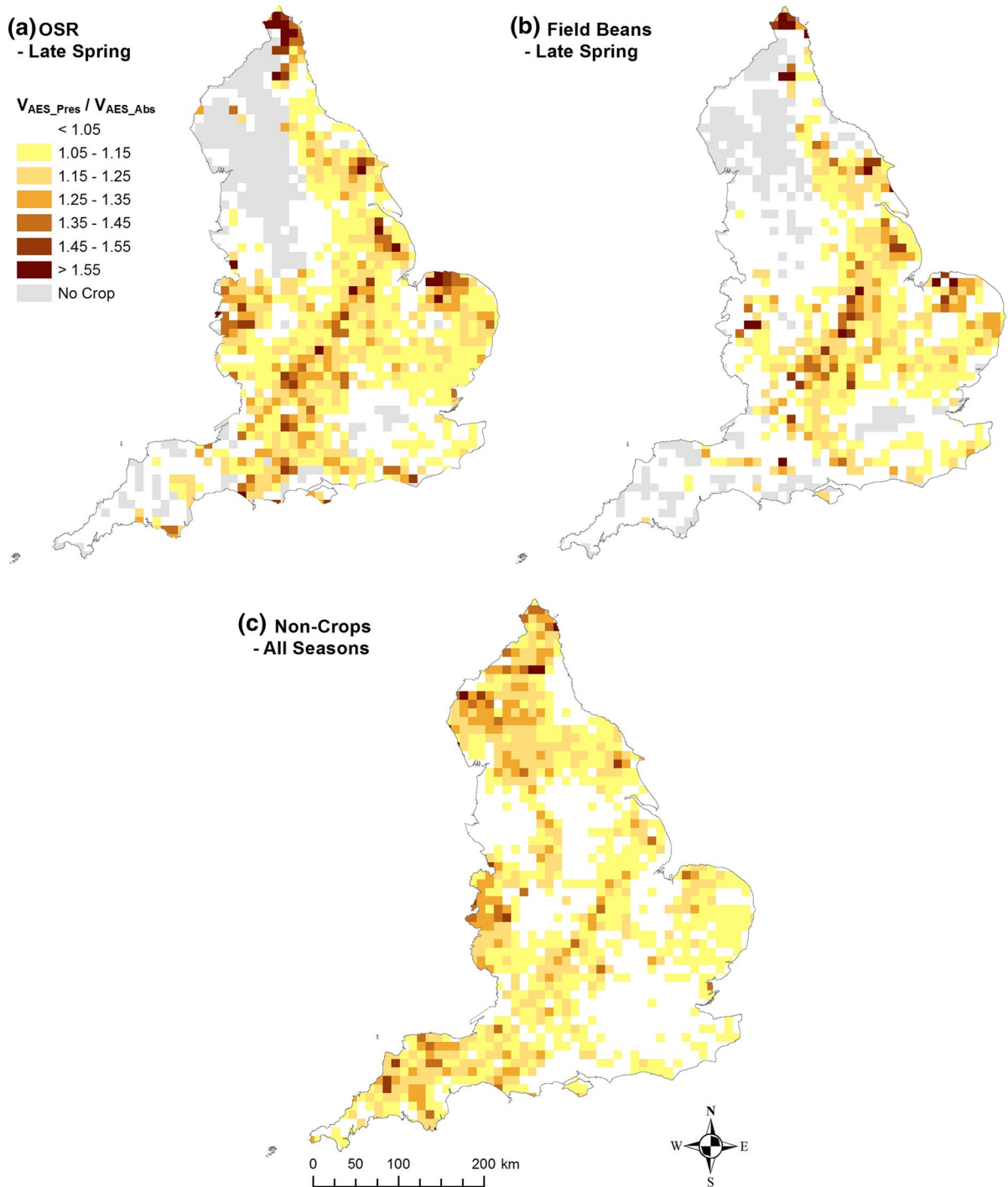


Fig. 2 Impact of AES on ground-nesting bumblebee visitation by 10 km tile for England in 2016 to **a** OSR (in late spring), **b** Field Beans (in late spring), and **c** Non-cropped areas (all seasons combined) as measured by the ratio of visitation in a

scenario where AES management is present (AES_Present) to a scenario where it is absent (AES_Absent). Tiles with <1% crop coverage (excluded from the regression analysis) are shown in grey

Table 1 Agri-environment scheme (AES) intervention categories, acronyms used for convenience in other tables/figures and broad descriptions of what intervention types in each group involve

AES Category	Acronym	Broad Description
Fallow	FA	Allow parts of or all of an arable field to go fallow
Floral margin	MF	Create a flower-rich margin or plot within a field
Grass margin	MG	Create a grass margin or plot within a field (floral richness not enhanced by sowing with wildflowers)
Hedgerow/woodland edge	HW	Create or manage hedgerows and woodland edges (woody linear features)
Flower-rich Ley	LE	Manage a field as a herb or legume-rich ley
Semi-natural habitat management	HM	Maintain existing semi-natural habitat with limited change in nesting or floral resource quality
Grassland/heath creation	GC	Create grassland (low-input or species-rich) or lowland heath from other land use
Scrub/wood creation	SC	Create scrub, successional areas, wood pasture or woodland from other land use
Traditional orchard creation	TC	Create traditional orchards from other land use
Wetland/coast creation	WC	Create wetland or coastal habitats from other land use

For full details of allocation of individual scheme management options (intervention) to group see Supplementary Material (Table S1)

wood pasture) as they have distinct floral and nesting resource values.

We chose to categorise interventions by change in early spring floral resource, rather than change in aggregate or other season floral resource, because empirical evidence suggests that wild bee populations are more sensitive to floral resource provision in early spring (Timberlake et al. 2019). Moreover, IM2022 predictions showed evidence of nesting resource limitation on crop visitation rate and predicted that mass flowering crop visitation by ground-nesting bumble-bee workers in late spring is strongly dependent on the resources available to the early-spring-foraging queens who produce these workers.

Determining relative contribution of each AES category to predicted change in visitation

We assumed that change in visitation rates at a 10 km tile level would be determined by the quantity of each AES category in the tile, with a different slope possible for each category. We determined the relative contribution of different AES categories to change in target crop visitation by stepwise backward Ordinary Least Squares (OLS) regression where the dependent variable was the visitation change ratio (change in visitation rate to target crop or non-crop land between *AES_Present* and *AES_Absent*) and the explanatory variables were the percentage cover of each AES category per 10 km tile (Table 2).

Because the dependent variable is a ratio of change in visitation, we also anticipated tiles with higher level of visitation in the *AES_Absent* scenario would be less responsive to area of AES. For this reason, we therefore included the proportion of “Non-Scheme Resource” in a tile as an interacting variable, where Non-Scheme Resource captured high resource quality land cover always outside the schemes in our study: this primarily covered suburban parks and gardens, woodland, and commercial orchards (Fig. 3k). We allowed the area of semi-natural habitat management AES variable to interact with other categories for the same reason. To account for the possibility that co-location of complementary resources might have an effect on the visitation ratio above and beyond summed effect of each intervention alone, we also allowed the following commonly co-located variables to interact in the regression: fallow, hedgerow/woodland edge, floral margin, grass margin.

A regression with the percentage area of AES feature in surrounding tiles as an additional explanatory variable was also trialled but this did not improve model fit (confirming that 10 km was an appropriate tile size for assessing bee population-level impacts) and so was dropped.

Although there was a strong positive correlation between the percentage cover of some AES categories (Fig. 5), variance inflation factors for all categories were below 5.00 (Supplementary Material Sect. 6). When fitting, we weighted by the inverse

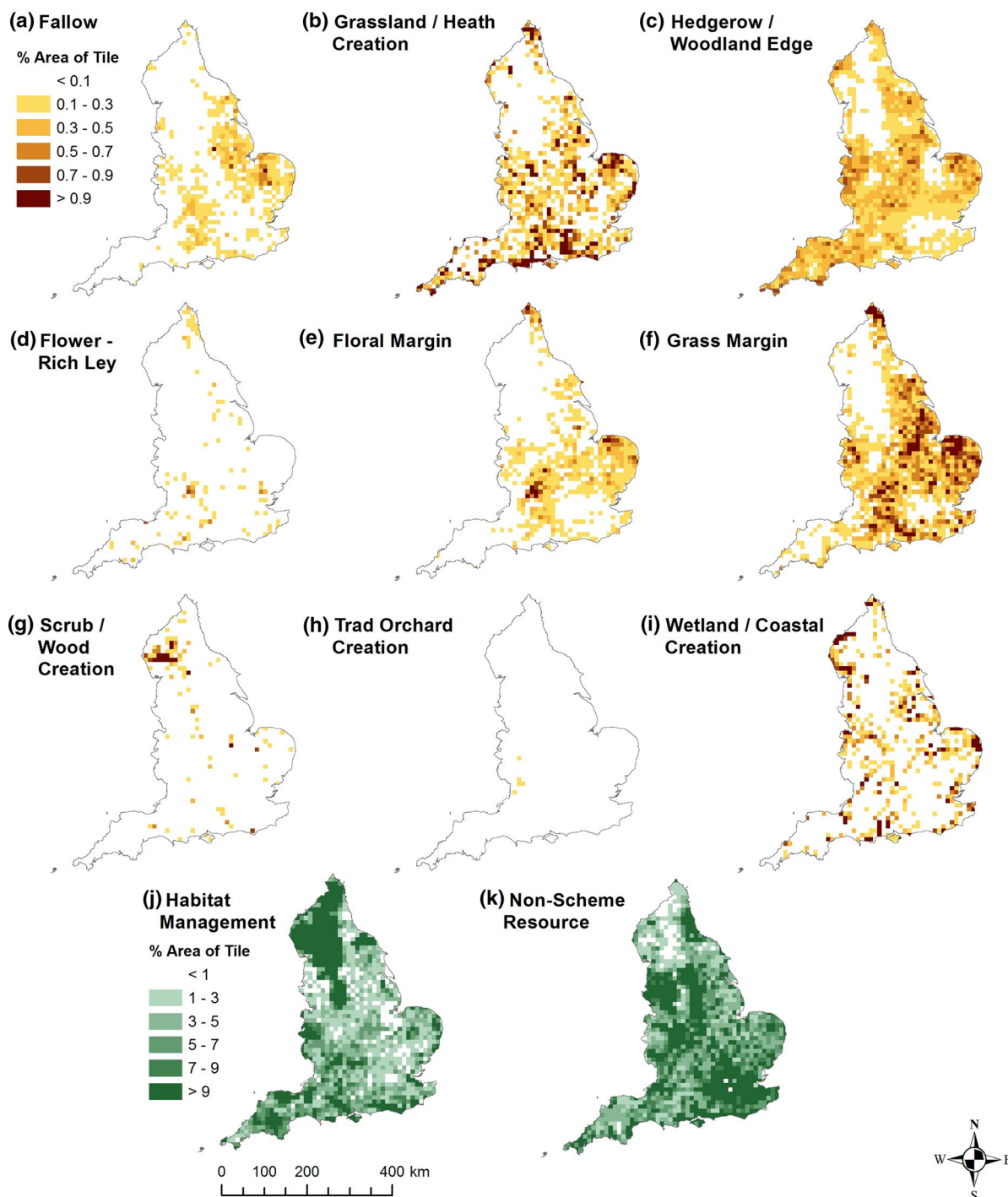


Fig. 3 Quantity of each AES category (a–j) and non-scheme resource (k) per 10 km tile for England in 2016. Non-scheme resource includes all habitat of value to wild bees outside AES

management including suburban parks/gardens, most commercial orchards and semi-natural habitat not entered into an eligible AES management option (mainly woodland)

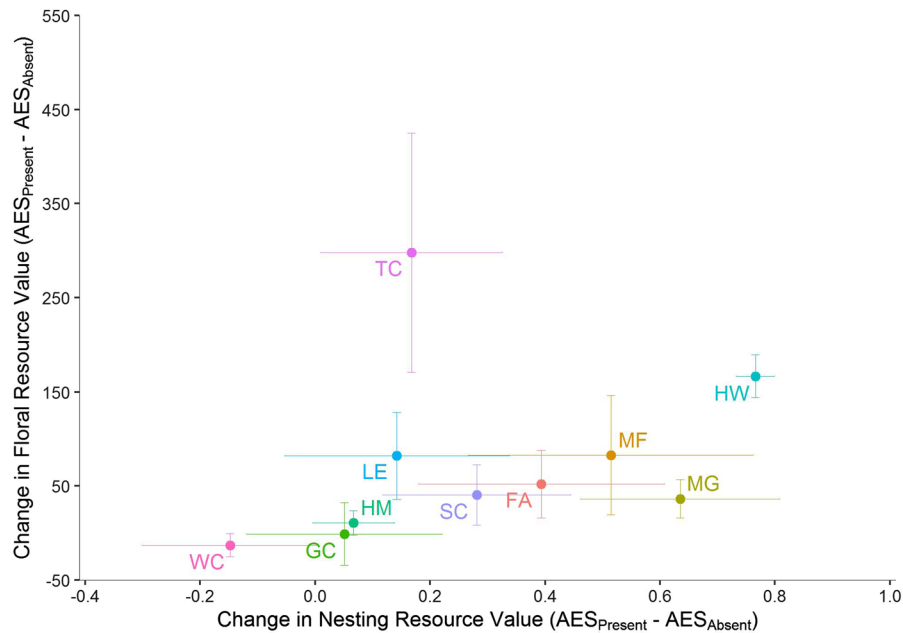


Fig. 4 Change in ground-nesting bumblebee mean nesting resource value and in mean early spring floral resource value for each agri-environment scheme (AES) category between scenario with AES management (AES_present) and without AES management (AES_absent). Values are weighted by the national proportion of land area taken up by each component for the reference year (2016). Horizontal and vertical bars represent the standard deviation of the mean nesting and floral

resource value respectively, also area weighted and incorporating error propagation (Hughes and Hase 2010). Categories are *FA* Fallow, *MF* Floral margin, *MG* Grass margin, *GC* Grassland/heath creation, *HM* Semi-natural habitat management, *HW* Hedgerow/woodland edge management, *LE* Flower-rich Ley, *SC* Scrub/wood creation, *TC* Traditional orchard creation, *WC* Wetland/Coastal habitat creation

of the standard deviation of the visitation ratio to account for uncertainty in the visitation rate change due to uncertainty in the poll4pop parameter inputs. A regression with the percentage of target crop in the tile as an interacting variable was also explored but this did not improve fit and so this variable was dropped.

Quality, quantity, and placement: identifying reasons for differing contribution of AES category

The regression coefficients produced for each AES category, where significant, indicate the change in relative visitation rate for a 1% increase in the area of that AES category in a 10 km tile. The size and direction of that coefficient is influenced by the change in nesting and floral resource provision per unit area for the AES category (quality) as well as the location of these interventions relative to the crop or non-crop areas being pollinated, and to other nesting

and floral resources (placement). The total quantity of uptake (by area) of an intervention nationally, as well as quality and placement, affect the significance of each coefficient: categories that provide high resource value and/or are well located may not result in significant effects if uptake is too low.

To disentangle the effects of quantity and quality, we plotted the size and significance of each AES category's regression coefficient against its logged mean area. of uptake per 10 km tile and against its change in resource quality. The change in resource quality of each AES category (Q_c) was calculated by normalising the per unit change in nesting resource ($N_c = N_{c(AES_Pres)} - N_{c(AES_Abs)}$) and per unit change in early spring floral resource ($F_c = F_{c(AES_Pres)} - F_{c(AES_Abs)}$) with respect to the minimum and maximum category values (N_{min} , N_{max} , F_{min} , F_{max}) (see Fig. 4) and multiplying these values together (Eq. 1). This multiplication approximated the process occurring in the poll4pop model.

Table 2 Description of variables used in the regression analysis

Variable	Description
Dependent	
Visitation ratio	Predicted average visitation to target cells within the tile in scenario where AES management is present / Predicted average visitation to target cells within the tile in scenario where AES management is absent
Explanatory	
Fallow (FA)	% area of tile in a fallow AES intervention
Grassland/heath creation (GC)	% area of tile in a grassland or heath creation AES intervention
Habitat management (HM)	% area of tile in a semi-natural habitat management AES intervention
Hedgerow/woodland edge (HW)	% area of tile in a hedgerow or woodland edge AES intervention
Flower-Rich Ley (LE)	% area of tile in a flower-rich ley AES intervention
Floral margin (MF)	% area of tile in a flower-rich margin AES intervention
Grass margin (MG)	% area of tile in a grass margin AES intervention
Scrub / wood creation (SC)	% area of tile in a scrub, woodland or wood pasture creation AES intervention
Traditional orchard creation (TC)	% area of tile in a traditional orchard creation AES intervention
Wetland/coastal creation (WC)	% area of tile in a wetland or coastal habitat creation AES intervention
Non-scheme resource (NSR)	% area of tile that contains potentially valuable habitat not in the schemes considered (primarily suburban parks and gardens, woodland and commercial orchards)
Interacting variables	
FA – HW – MF – MG	Mutual 2-way interactions only
NSR	Interactions with all other explanatory variables
HM	Interactions with all other explanatory variables

$$Q_c = (N_c - N_{min})(N_{max} - N_{min}) * (F_c - F_{min})(F_{max} - F_{min}) \quad (1)$$

The influence of placement was then inferred by considering the size and significance of the regression coefficient with respect to change in resource quality and the mean area of uptake, and by cross-referencing with the spatial correlations shown in Fig. 5. An AES category whose coefficient is larger than might be expected for the change in resource quality may indicate one that is better located with respect to the crop or non-crop of interest. Whereas poor placement of an AES category may explain the lack of a significant effect despite having reasonable uptake and providing good quality resource. Significant interactions in the regression would also indicate whether the effect of an AES category was influenced by prior landscape context (i.e., availability of non-scheme resource) or co-location with other AES categories with different resource quality.

Tools

Data processing was carried out in Python 2.7 / 3.5 and R (R Core Team 2018). Map outputs were produced in ArcGIS 10.7 (ESRI 2019).

Results

Relative contribution of each AES category to predicted change in visitation

Of the four bee guilds assessed, only ground nesting bumblebees showed widespread and significant increases in OSR and field bean visitation due to AES management at a national scale (IM2022). Hence, as noted above, we present below results for this guild only (for results for other guilds, see Supplementary Material Table S3–5).

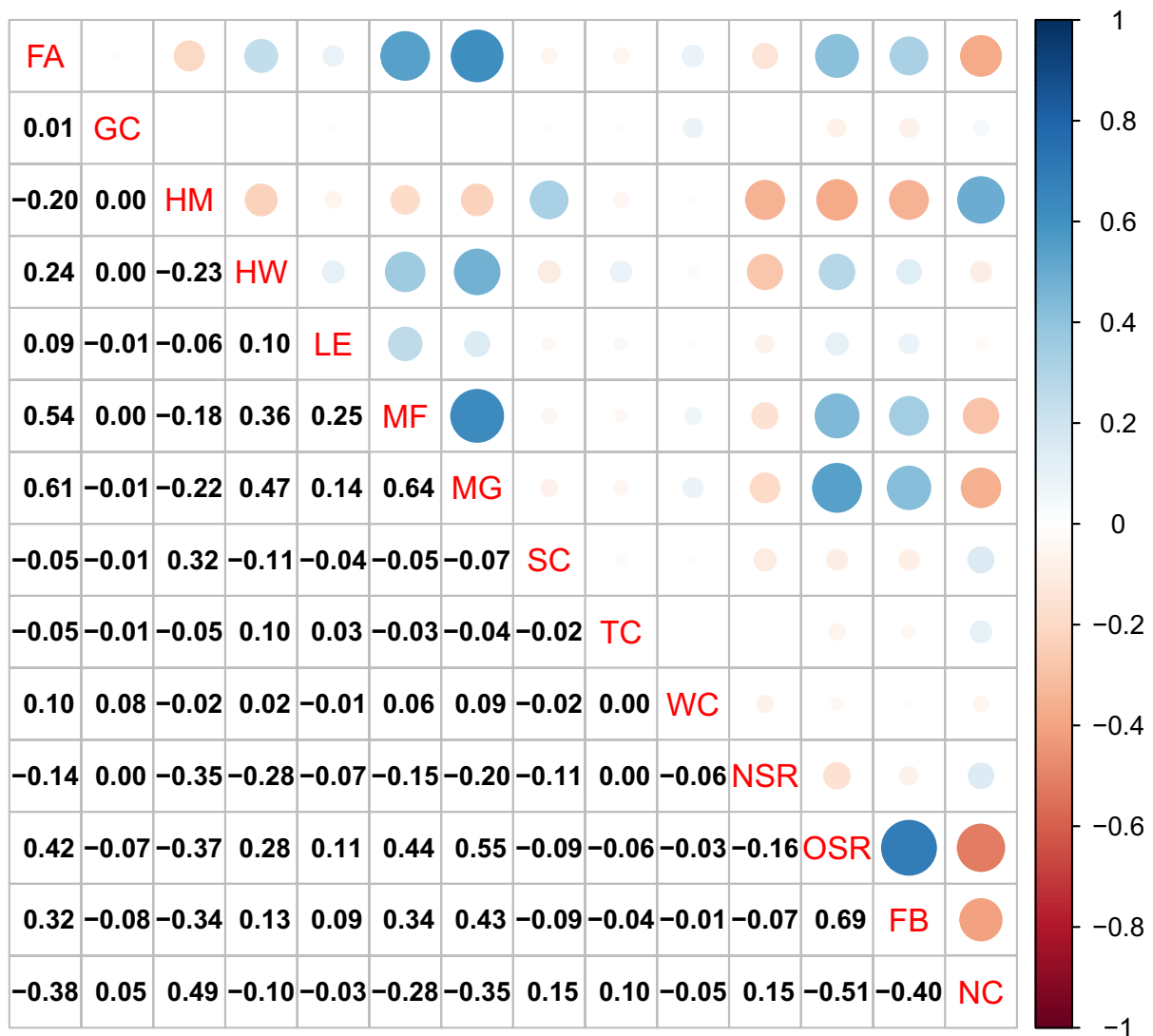


Fig. 5 Correlation Matrix, % Area of Tile: Categories are *FA* Fallow, *MF* Floral margin, *MG* Grass margin, *GC* Grassland/heath creation, *HM* Semi-natural habitat management, *HW* Hedgerow/woodland edge management, *LE* Flower-rich Ley, *SC* Scrub/wood creation, *TC* Traditional orchard Creation, *WC* Wetland/coastal habitat creation, *NSR* Non-scheme resource,

OSR Oilseed rape, *FB* Field beans, *NC* Non-cropped areas. Cells below the leading diagonal show correlation coefficients whilst cells above indicate the same information as colour code (blue=positive, red=negative) and shade/size (larger values are represented by larger discs with darker shades)

Crop visitation

There are significant positive relationships between the area of fallow, habitat management, hedgerow/woodland edge, and grass margin categories within a tile and the predicted change in visitation rate to both crops for ground-nesting bumblebees (Table 3; See Supplementary Material for other guilds). Of

these four AES categories, hedgerows/woodland edge has the largest effect size: a 1% increase in cover between *AES_Present* and *AES_Absent* scenarios accounts for a 0.33 (± 0.02) and 0.26 (± 0.02) proportional increase in relative predicted visitation rate to OSR and field bean, respectively. Fallow cover has a stronger positive association with change in field bean visitation than change in OSR visitation (0.17 ± 0.04

Table 3 Results for linear regression for ground-nesting bumblebee visitation ratio (visitation per tile to target land class (season) with AES features present / visitation per tile to target land class (season) with AES features absent) to each of OSR

(late spring), Field Beans (late spring) and non-crops (all seasons) as a function of percentage composition of different AES categories in landscape tiles (see Table 2 for definitions of all response and explanatory variables)

Variable	OSR	Field beans	Non-crop
(Intercept)	$0.99 \pm 0.01^{***}$	$0.99 \pm 0.01^{***}$	$1.0E-4 \pm 9E-5^{***}$
Fallow (FA)	$0.09 \pm 0.03^{***}$	$0.17 \pm 0.04^{***}$	
Grassland/Heath Creation (GC)	$0.019 \pm 0.007^{**}$		$-0.008 \pm 0.001^{***}$
Habitat Management (HM)	$0.0016 \pm 0.0003^{***}$	$0.0025 \pm 0.0004^{***}$	$0.0023 \pm 0.0001^{***}$
Hedgerow/Woodland Edge (HW)	$0.33 \pm 0.02^{***}$	$0.26 \pm 0.02^{***}$	$0.29 \pm 0.01^{***}$
Flower-Rich Ley (LE)	-0.053 ± 0.034	-0.043 ± 0.039	$0.08 \pm 0.03^{**}$
Floral Margin (MF)	$0.12 \pm 0.03^{***}$	0.008 ± 0.048	$0.11 \pm 0.03^{***}$
Grass Margin (MG)	$0.10 \pm 0.02^{***}$	$0.12 \pm 0.02^{***}$	-0.010 ± 0.006
Scrub / Wood Creation (SC)			$0.03 \pm 0.01^*$
Trad. Orchard Creation (TC)			
Wetland/Coastal Creation (WC)	$-0.0076 \pm 0.0034^*$	0.0025 ± 0.0049	$-0.012 \pm 0.002^{***}$
Non-Scheme Resource (NSR)	$0.0006 \pm 0.0002^{***}$	$0.00042 \pm 0.00001^{**}$	$0.0E-6 \pm 2E-7$
GC* NSR	$-0.0006 \pm 0.0002^{**}$		
HW* NSR	$-0.013 \pm 0.001^{***}$	$-0.0075 \pm 0.0015^{***}$	$-0.0100 \pm 0.006^{***}$
LE* NSR			$-0.0039 \pm 0.0019^*$
MF* NSR	$-0.005 \pm 0.002^*$		$-0.0033 \pm 0.0013^{**}$
FA* HM	$0.012 \pm 0.004^{**}$		
GC* HM	$-0.0008 \pm 0.0004^*$		
HM* LE	$0.026 \pm 0.005^{***}$	$0.030 \pm 0.007^{***}$	
HM* MF		$0.009 \pm 0.003^{**}$	
HM* MG	$0.0029 \pm 0.0013^*$		$0.0034 \pm 0.0006^{***}$
HM* WC		$-0.00064 \pm 0.00026^*$	
HW* MF			$-0.19 \pm 0.05^{***}$
FA* MG	$-0.14 \pm 0.04^{**}$	$-0.18 \pm 0.04^{***}$	
N	1189	1195	1496
R ²	0.73	0.68	0.74

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

vs 0.09 ± 0.03 increase in relative predicted visitation rate per 1% increase in area). Change in coverage of habitat management interventions has only a very weak positive relationship with the net change in relative predicted visitation rate (0.0016 ± 0.0003 (OSR), 0.0025 ± 0.0004 (field beans)).

Relationships between area of other AES categories in a tile and net change in relative predicted crop visitation rates are less consistent. The predicted change in relative OSR visitation rate is positively dependent on area of floral margin ($+0.12 \pm 0.03$) and grassland/heath creation ($+0.019 \pm 0.007$) but shows no relationship with scrub/woodland creation cover. In contrast, change in relative field bean visitation rate shows no significant relationship with the

area of any of these categories. There is no significant relationship between cover of flower-rich ley or traditional orchard creation with change in relative predicted visitation rate to either crop. Wetland/coastal habitat creation has a slightly negative relationship (-0.0076 ± 0.0034) with change in OSR visitation but not field beans.

Examination of statistical interactions shows that increasing the area of non-scheme resource in a tile significantly weakens the positive relationship between area of certain AES categories (hedgerow/woodland edge, floral margins, grassland/heath creation) and predicted change in crop visitation rate (Table 3; Figs. S4a–c, S5a–c). The positive effect on crop relative visitation rate of increasing fallow

coverage is enhanced when there is more semi-natural habitat management also present (Figs. S4d, S5d) in the tile but is diminished when there are larger areas of grass margin (Figs. S4g, S5f–g). The positive effect on crop relative visitation rate of increasing grassland/heath cover is also enhanced when there is more semi-natural habitat management present. The positive effect of semi-natural habitat management on change in crop visitation is enhanced where flower-rich ley, floral margin and grass margin cover is higher, but reduced where wetland/coastal habitat creation is higher.

Non-crop visitation

As with the crop visitation predictions, there was also a significant positive relationship between predicted relative non-crop visitation rate and the area of hedgerow/woodland edge ($+0.29 \pm 0.01$). There were also significant, but weaker, positive relationships with area of floral margin ($+0.11 \pm 0.03$), flower-rich ley ($+0.08 \pm 0.03$), scrub/wood creation ($+0.03 \pm 0.01$) and semi-natural habitat management ($+0.0023 \pm 0.0001$) interventions, whilst increasing the cover of wetland creation (-0.01 ± 0.002) and grassland heath creation interventions (-0.008 ± 0.001) each have small but significant negative effects. Unlike mass flowering crops, there is no significant relationship between change in relative visitation rate and the quantity of fallow or grass margin interventions.

Again, the positive relationship between relative non-crop visitation rate and quantity of certain AES categories (hedgerow/woodland edge, floral margin, and flower-rich ley) is significantly weaker for higher areas of non-scheme resource (Table 3; Fig. S6a–c). The positive effect of hedgerow/woodland edge is also reduced in the presence of greater areas of floral margin edge ($HW*MF - 0.19 \pm 0.05$). However, there is a positive interaction between area of grass margin and area of semi-natural habitat management ($MG*HM + 0.0034 \pm 0.0006$).

Quantity, quality, and placement: differing contribution to change in pollination service by AES category

Categories with lower quantity (area of uptake) nationally tend to be those which do not have a

significant effect on the net change in visitation rate (Fig. 6a, c, e), e.g. traditional orchard creation (both crops and non-crop) and flower-rich ley (both crops). Area of uptake appears to be a more important factor in determining significance of effect on change in visitation to crops than non-crops (compare Fig. 6a, c vs. e). Categories with greater resource added value (quality) such as grass margins, floral margins, hedgerow/woodland edge and fallow tend to have more positive marginal effects on net change in relative visitation rate (Fig. 6b, d, f) across both crops and non-crops.

Placement effects were inferred for: fallow (much higher regression coefficient than interventions of similar quality and quantity indicating effective placement), grassland/heath creation and floral margins (significant positive effect for OSR and non-crop visitation but not for field beans inferring differential placement), grass margins (significant positive effect for OSR and field bean visitation but not for non-crops also inferring differential placement), flower-rich ley and scrub/woodland creation (significant positive effect for non-crop visitation but not for either crop also inferring differential placement).

Discussion

IM2022 (Image et al. 2022) used a spatially explicit process-based model to simulate foraging and population processes of wild bees and predict the net change in bee visitation due to the suite of AES interventions under active management in England during 2016, compared to a land-use scenario where these interventions were absent. In this study, we used linear regression to determine which of the implemented AES interventions (aggregated by category) are driving the predicted changes in relative visitation to OSR, field beans and non-crop areas and why. We focussed our analysis on ground-nesting bumblebees as this was the only guild to show a widespread and significant response in OSR and field bean visitation rates due to AES management in IM2022.

In general, the AES categories with larger area of uptake are the ones with significant effects on change in ground-nesting bumblebee visitation. Of

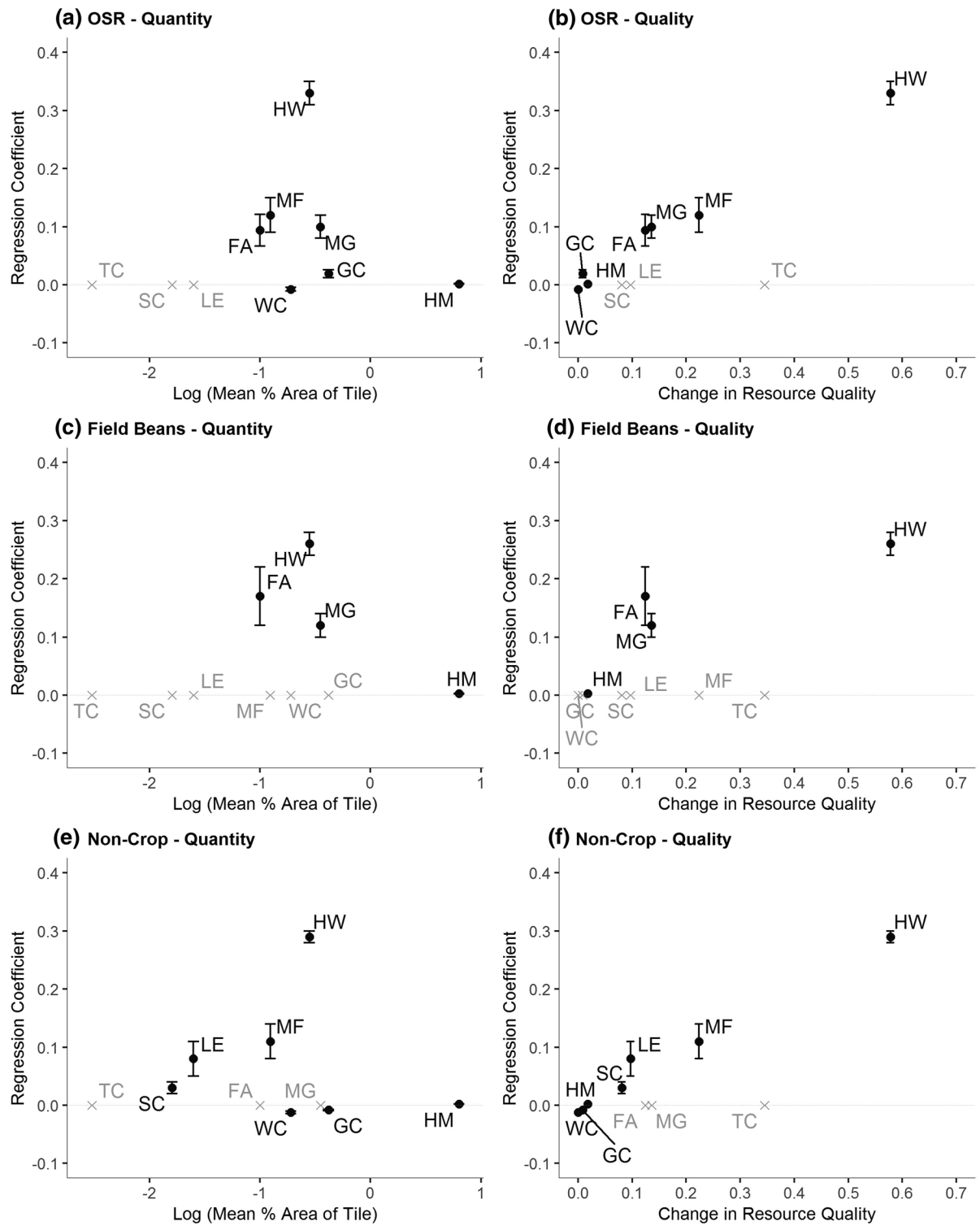


Fig. 6 Magnitude of regression coefficient (representing change in predicted ground-nesting bumblebee relative visitation rate between scenario with AES present and scenario with AES absent per unit area of intervention) as a function of national quantity of AES category (measured as the log of the mean percentage intervention area per 10 km tile recorded in the year 2016) for OSR (**a**), Field beans (**c**) and Non-crop (**e**). Magnitude of regression coefficient as a function of quality of AES category (normalised change in nesting quality * normalised change in early spring floral quality) for OSR (**b**), Field Beans (**d**) and Non-Crop (**f**). Categories are *FA* Fallow, *MF* Floral margin, *MG* Grass margin, *GC* Grassland/heath creation, *HM* Semi-natural habitat management, *HW* Hedgerow/woodland edge management, *LE* Flower-rich Ley, *SC* Scrub/wood creation, *TC* Traditional orchard creation, *WC* Wetland/coastal habitat creation. Black points denote significant regression coefficients with standard errors. Crosses denote intervention categories with no significant regression coefficient

those, the ones that provide higher relative nesting and floral resource quality tend to have a greater effect on the net change in visitation. However, the results also reveal differences between AES categories in terms of significance and magnitude of their visitation effects across crop type and non-crops. These suggest placement effects, mutual interactions and other factors which also have important implications for scheme design.

Hedgerow and woodland edge management

Our results suggest that the predicted increases in both mass-flowering crop and non-crop relative visitation due to the AES participation are strongly dependent on the area of hedgerow and woodland edge interventions in a tile. The magnitude of the increases predicted reflects empirical evidence (Bailey et al. 2014; Sutter et al. 2018) and is likely linked to the high resource quality. AES management provides greater nesting opportunity for ground-nesting bumblebees as well as greater early-spring floral resource, factors which are more critical for population growth than floral resource provision in late spring or summer seasons (Carvell et al. 2017; Timberlake et al. 2019). Whilst hedgerows and woodland edges outside of AES can also be of value to wild bees, they can either be overmanaged (reducing floral cover) or under-managed (compromising structural integrity). AES managed features are cut at a specific frequency that maintains structural integrity without compromising floral cover (Staley et al. 2012). We approximated this effect in the model by allowing

AES features to be twice the width of a feature outside the scheme, so our prediction does rest on the assumption that features under an AES regime effectively provide twice as much resource quality. However, visitation rate changes of this order are observed empirically (Byrne and delBarco-Trillo 2019).

The consistency of the predicted net visitation rate change to both crops and non-crops is likely because these interventions have high uptake area across both arable and non-cropped landscapes (compare Fig. 3c to 2). They may also be providing ecological connectivity from resource-limited cropping areas to resource-rich existing semi-natural habitat features (Sullivan et al. 2017). Maintaining this extent of hedgerow/woodland edge management in future schemes will therefore be important in supporting pollination services (Albrecht et al. 2020). In principle, the beneficial effect could be enhanced by planting new hedgerows to further extend the hedgerow network, though it may take over five years for these to provide resources of equivalent quality to mature hedgerows (Kremen et al. 2018).

Floral and grass margins

We predict that floral margins have positively affected the change in relative visitation to OSR and non-cropped areas due to overall AES participation but have not had a significant effect on relative field bean visitation. The magnitude of their effect on OSR and non-crops is much smaller than hedgerow/woodland edge but is consistent with a more limited resource quality (Fig. 6). Although floral margins include wildflowers in their seed mix, the parameterisation in the model reflects that the species selected in schemes provide most floral resources in the summer season with very limited spring provision (Ouvrard et al. 2018). The lack of significant effect on field beans suggests a placement factor where there are insufficient floral margin interventions near field bean parcels to result in a significant effect. This may simply be because the area covered by floral margins is not sufficiently high to enhance bee populations consistently across the landscape (Carvell et al. 2015), so field beans (which are rarer in the landscape than OSR and non-crop features; Fig. 1) are less likely to be co-located.

Our predictions suggest that grass margins have positively affected the change in relative visitation to

OSR and field beans due to overall AES participation but have not had a significant effect on net non-crop visitation. The magnitude of their effect on crops is also consistent with their resource quality (Fig. 6). Grass margins can still provide an important nesting resource for ground-nesting bumblebees but do not achieve the same floral resources as interventions explicitly sown with wildflowers (hence their lower parameterisation), and the species which establish will also tend to be summer flowering. However, they are a very popular intervention covering a large area (Fig. 3f) which likely allows them to influence field bean visitation as the chance of co-location is high. Grass margins are negatively correlated with non-crops (-0.35 ; Fig. 5), but placement is not a complete explanation for the lack of significant effect on non-crops as floral margins also have a negative correlation (-0.28). Low resource quality may also be a factor as visitation rates to non-crop in the *AES_Absent* scenario may be already high, so grass margins are unable to add sufficient additional visitation to be significant.

Grass margins are playing an important role in supporting the crop pollination services provided by the overall schemes and should continue to be incentivised. Floral margins are also valuable but could support more pollination of sparsely distributed crops if they were more abundant in the landscape. Another potential enhancement to the floral margin intervention would be to incorporate species in the sowing mix which come into flower before mass-flowering crops, such as primrose (*Primula vulgaris*), cowslip (*Primula veris*) and red campion (*Silene dioica*) (Nowakowski and Pywell 2016). This would help sustain larger wild bee populations and further enhance pollination service. A similar effect could be achieved more generally by land users by tolerating some early-flowering perennial weeds such as dandelion (Hicks et al. 2016) which has been identified as a strong predictor of pollinator abundance in urban habitats (Baldock et al. 2019).

Fallow

Our results suggest that the predicted increases in visitation to both mass-flowering crops due to the AES participation are dependent on the area of fallow interventions in a tile. Fallow interventions have a similar net resource quality as grass margins in our

parameterisation (Gardner et al. 2020) and the magnitude of the effect on OSR is very similar. Like grass margins, fallow also has a strong negative correlation with non-crop areas (-0.35 ; Fig. 5) so it is likely that the lack of significant effect on non-crops is driven by the same factors as those already discussed for grass margins. However, the effect of fallow on net field bean visitation is stronger than would be expected from resource quality alone even though area of fallow is more strongly correlated at tile level with area of OSR than area of field beans. This suggests that fallow interventions are being located more efficiently with respect to field bean parcels than other interventions though this may be an inadvertent consequence of landholder decision-making.

The fallow category comprises a range of interventions that create non-cropped areas within arable rotations, sometimes for specific biodiversity objectives (e.g., plots for ground-nesting birds) and our simulations support site-specific observational evidence that fallow options represent an important asset in the context of ecosystem service delivery by supporting crop pollination and farmland bird populations simultaneously (Ouvrard and Jacquemart 2018). Temporary features such as fallow plots may be particularly valuable contributors to crop pollination in more intensive arable contexts where there is less land given up to longer-term or permanent semi-natural features like field margins or hedgerows. These interventions should continue to be promoted in future schemes.

Tree planting

Scrub/woodland creation interventions (representing conventional woodland creation but also including successional habitat creation) do not have a significant effect on the net change in mass-flowering crop visitation rate due to overall AES participation but do have a small but significant positive effect on net non-crop visitation by ground-nesting bumblebees. The quantity of these interventions is very low in more intensively farmed areas (compare Fig. 3g to Fig. 2) so it is not surprising to see no significant crop effect. The magnitude of the non-crop effect is in line with the limited scale of increase in resource quality that scrub/woodland creation provides to this guild. However, this does not take into consideration the woodland edge effect (which is grouped with hedgerow) so

woodland creation may be providing a greater service than our categorisation suggests.

Traditional orchard creation has no effect on either crop or non-crop net visitation, most likely because the quantity is very limited. This is a missed opportunity to significantly enhance pollination service because fruit trees have very high early spring visitation and so could potentially support higher wild bee populations whilst not competing with later flowering crops or habitats for bee visitation. Realistically, traditional orchards have geographical constraints and are unlikely to be taken up in more intensive arable areas. Instead, English AES could increase the quantity of fruit trees (and other early-flowering trees such as willow) by promoting silvoarable agroforestry (e.g., alley cropping with fruit trees or willow). This was not supported in the schemes studied but might be highly valuable due to early season floral resource quality and potential for co-location with mass flowering crops (Varah et al. 2020; Staton et al. 2022). Fruit-tree based agroforestry systems also provide a range of other ecosystem services beyond pollination (Kay et al. 2018).

Other interventions

Semi-natural habitat management interventions are predicted to have a significant positive effect on net visitation to crops and non-crops due to overall AES participation, but the magnitude of the effect is very small. As the category name suggests the focus is on management rather than enhancement and as such they tend to only slightly increase resource quality (Berg et al. 2019), as reflected in our parameterisation. However, their high uptake means they are making small changes over a large area, and they often enhance the effects of other categories. For instance, nearby semi-natural habitat management supports the positive effects of higher value interventions (e.g. fallow, flower-rich ley, grass and floral margins; see interaction effects in Table 3).

Our simulations also suggest that grassland/heath creation interventions have a small but significant positive effect on net OSR and non-crop visitation but not on field beans (likely for similar reasons as suggested for floral margins). Again, the magnitude of effect is consistent with change in resource quality which is small in our parameterisation. This may be because only a small proportion of the

interventions within this category are higher quality types like “Creation of species-rich grassland—GS8” (Table S1). These are potentially being diluted by “Restoration of Lowland Heath—HO2”, a popular ES management option with more limited overall floral resource change as it requires some scrub removal to promote heather regeneration. Moreover, our simulations focus on ground-nesting bumblebees and are at the guild level. As such, they do not capture the vital role that grassland/heath creation interventions (and related semi-natural habitat management, discussed above) can play in maintaining wild bee species richness (Rotchés-Ribalta et al. 2018). As pollinator species richness can be as valuable as abundance to maintaining reliable pollination services (Woodcock et al. 2019), these interventions should continue to be supported.

Our simulations predict that flower-rich leys currently significantly influence net non-crop visitation but not crop visitation due to low uptake (Fig. 4d). They offer similar floral quality to floral margins, but this is also mainly expressed in the summer months when the clover and other forbs that are in the specified sowing mixes will flower. Their effect may also be smaller in magnitude relative to floral margins as they have a lower nesting quality (greater disturbance is expected). Nevertheless, if uptake were greater within arable rotations, they may potentially be able to contribute to mass-flowering crop visitation.

Targeting interventions at landscape-scale and farm-scale

Our simulations demonstrate significant landscape-scale negative interactions between the implemented AES interventions and area of non-scheme resource. This implies there is spatial heterogeneity in intervention effectiveness, where interventions are more effective in simplified landscapes in which the baseline visitation rate is lower, consistent with theories of landscape moderation of ecological process (Tscharntke et al. 2005, 2012). This suggests scheme designs should consider quantity of non-scheme resource and pre-existing habitat management to effectively target interventions at areas with limited pre-existing nesting or floral resources, if supporting wild and crop pollination services is a desired outcome.

Interactions between individual interventions are driven by nesting/foraging choices of our simulated

bees at the farm scale. In arable areas with few grass margins, bees rely on fallow areas for nesting producing a positive relationship between fallow area and change in crop visitation rate in our simulations. Where there are more grass margins, bees preferentially use these for nesting due to their higher nesting resource value in our parameterisation (Fig. 4), hence weakening this relationship with fallow area (interaction effect; Fig. S4h, Fig. S5e). A similar interaction effect occurs between floral margins (summer flowering) and hedgerows (early spring flowering) on non-crop visitation (Fig. S6e). This is likely due to the complementarity of their floral resources meaning bees nesting in close proximity to both features no longer need to access nearby non-crop areas (e.g. semi-natural habitats) for resources. These interactions emphasise the importance of landholders considering complementarity and current level/limitations in resource provision on their land when choosing suites of interventions in order to maximise benefits for food production and for nearby natural habitats.

Limitations and implications for future research

The limitations of the poll4pop model and its application to English AES are discussed in IM2022. As the outputs of that paper are used as the inputs to this study, the same caveats (season-level temporal resolution, generalisation of species to guild, and relationship between visitation rate and yield) will also apply. Finer temporal resolution in particular would better capture the important early-season resource quality provided by the hedgerow/woodland edge category, so that it may emerge as an even stronger driver of visitation rate change. Inclusion of a late summer (e.g. August/September) season in the model would also have allowed us to represent the later ‘hunger gap’ (Timberlake et al. 2019) and so may have increased the relative contribution of floral margins and flower-rich ley categories to visitation rate change where interventions include later flowering plants such as red clover (*Trifolium pratense*).

In this study, 364 AES interventions are categorised into 10 categories to simplify the regression analysis. This results in intervention categories which occupy distinct positions in ground-nesting bumblebee nesting-floral resource quality space, but with error bars which do overlap indicating that the

classification is not perfect (see Fig. 4). We have already highlighted how our approach may understate the value of certain interventions in the grassland/heathland creation category (i.e., “Creation of species-rich grassland—GS8”). More work is needed to determine how individual interventions are contributing to overall scheme effectiveness. We do not report effect sizes for non-significant variables (e.g., traditional orchards, scrub/woodland creation for relative crop visitation), as per standard statistical process. The p-value threshold is useful for identifying AES categories whose effect on relative visitation is uncertain due to low uptake or ineffective placement, but we acknowledge the limitation of p-values here given the slight lack of independence between explanatory and dependent variables.

We investigated which interventions are the strongest drivers of the change in visitation rate that occurs at 10 km scale when the whole scheme was implemented. While our results are informative for improving national and regional scheme design/targeting, individual land managers may ultimately benefit most from interactive tools that present the local potential of interventions to improve visitation in their specific locality. More research is needed to develop the poll4pop model so it can be more readily embedded into user-friendly, practitioner-focused, landscape decision-making tools and this may in turn help to improve intervention uptake.

Conclusions and recommendations

Our study disentangles the contributions of different intervention types implemented within agri-environment schemes (AES) in England in 2016 to predicted impacts on ground-nesting bumblebee pollination services to OSR, field beans and the wider landscape. We find intervention categories with high area of uptake and those offering high resource quality (specifically nesting and early spring resource provision) typically had most influence on the schemes’ net effect on pollination services. We also show that placement matters for some interventions, with their location relative to crops, other AES interventions and pre-existing habitat influencing their effectiveness for supporting pollination services.

Based on our findings, we make the following recommendations for improving the design of future

agri-environment schemes to better support wild and crop pollination services.

- Promote hedgerow and woodland edge management: These interventions offer good nesting and floral resources (especially early in the year) and have a strong effect on pollination services to crops and non-crop areas alike, due to wide uptake and high landscape connectivity.
- Include more early flowering species in floral margins and increasing their uptake in the landscape: Floral margins provide high floral resource in summer but little in early spring, so adding early flowering species may increase pollination service benefits. Greater uptake will better enable these valuable features to support pollination service to important but less frequently planted crops such as field beans.
- Promote fallow interventions in intensively managed landscapes: Fallow features do not require long-term land use change so can be easily incorporated into rotations in intensive arable landscapes where baseline pollination service is lower. Our findings show they provide an efficient multifunctional asset, significantly supporting bees in addition to their more commonly bird-focused objectives.
- Promote tree creation in arable landscapes: Our simulations already highlighted the potential pollination service benefits of linear/elongated management interventions. Increasing tree cover (especially hedgerows and agroforestry systems) can provide further nesting and early floral resource value.
- Consider landscape context at different scales when targeting uptake: Current interventions are predicted to be more effective in landscapes with lower quantities of pre-existing habitat. At farm scale, our simulations indicate that encouraging co-location of interventions with complementary nesting and early spring floral resource quality is likely to increase their effectiveness.

Author contributions MI conceived the ideas, carried out the research and wrote the manuscript. TB, EG, GS and HS 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.

Funding MI was funded by a Wilkie Calvert co-supported PhD studentship from the University of Reading. This research was also supported by the grant “Modelling Landscapes for Resilient Pollination Services” (BB/R00580X/1), funded by the Global Food Security ‘Food System Resilience’ Programme, which is supported by BBSRC, NERC, ESRC and the Scottish Government.

Data availability The process-based pollinator model is freely available to download at: https://github.com/imagema/poll4pop_python (<https://doi.org/10.5281/zenodo.5680076>). The values of the dependent variable and independent variables for each 10 km tile used in the linear regression are available in the Supplementary Material.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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