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RESEARCH ARTICLE

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Field boundary features can stabilise bee populations and the pollination of mass-flowering crops in rotational systems

Emma Gardner[1,2] | Tom D. Breeze[2] | Yann Clough[3] | Henrik G. Smith[3] | Katherine C. R. Baldock[4,5,6] | Alistair Campbell[7] | Michael P. D. Garratt[2] | Mark A. K. Gillespie[8,9] | William E. Kunin[8] | Megan McKerchar[10] | Simon G. Potts[2] | Deepa Senapathi[2] | Graham N. Stone[11] | Felix Wäckers[12] | Duncan B. Westbury[10] | Andrew Wilby[12] | Tom H. Oliver[1]

[1]School of Biological Sciences, University of Reading, Reading, UK; [2]Centre for Agri-Environmental Research, University of Reading, Reading, UK; [3]Centre for Environmental and Climate Research and Department Biology, Lund University, Lund, Sweden; [4]School of Biological Sciences, University of Bristol, Bristol, UK; [5]Cabot Institute, University of Bristol, Bristol, UK; [6]Department of Geographical and Environmental Sciences, Northumbria University, Newcastle upon Tyne, UK; [7]Laboratório de Entomologia, Embrapa Amazônia Oriental, Belém, Brazil; [8]School of Biology, University of Leeds, Leeds, UK; [9]Department of Environmental Sciences, Western Norway University of Applied Sciences, Sogndal, Norway; [10]School of Science and the Environment, University of Worcester, UK; [11]Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK and [12]Lancaster Environment Centre, Lancaster University, Lancaster, UK

Correspondence
Emma Gardner
Email: emmgar@ceh.ac.uk

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Abstract

1. Pollinators experience large spatiotemporal fluctuations in resource availability when mass-flowering crops are rotated with resource-poor cereal crops. Yet, few studies have considered the effect this has on pollinator population stability, nor how this might be mitigated to maintain consistent crop pollination services.
2. We assess the potential of boundary features (standard narrow 1 m grassy margins, hedgerows and wide 4 m agri-environment margins) to support and stabilise pollinator populations and pollination service in agricultural landscapes under crop rotation. Assuming a 6-year rotation, we use a process-based pollinator model to predict yearly pollinator population size and in-crop visitation rates to oilseed rape and field bean across 117 study landscapes in England with varying amounts of boundary features. We model both ground-nesting bumblebees and solitary bees and compare the predictions including and excluding boundary features from the landscapes.
3. Ground-nesting bumblebee populations, whose longer-lifetime colonies benefit from continuity of resources, were larger and more stable (relative to the no-features scenario) in landscapes with more boundary features. Ground-nesting solitary bee populations were also larger but not significantly more stable, except with the introduction of wide permanent agri-environment margins, due to their shorter lifetimes and shorter foraging/dispersal ranges.

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4. Crop visitation by ground-nesting bumblebees was greater and more stable in landscapes with more boundary features, partly due to increased colony growth prior to crop flowering. Time averaged crop visitation by ground-nesting solitary bees was slightly lower, due to females dividing their foraging time between boundary features and the crop. However, despite this, the minimum pollination service delivered was higher, due to the more stable delivery.
5. *Synthesis and applications*. Field boundary features have an important role in stabilising pollinator populations and pollination service in rotational systems, although maintenance of larger semi-natural habitat patches may be more effective for stabilising less mobile solitary bee populations. We recommend using combinations of boundary features, accounting for pollinator range when spacing features/rotating crops, and synchronising boundary feature management with crop rotation to maximise their stabilising benefits.

KEYWORDS

agroecology, crop rotation, field margins, hedgerows, pollinators and pollination service, resilience, stability, variability

1 | INTRODUCTION

Pollination is a key ecosystem service to global agriculture, enhancing production in ~75% of global crop species (Klein et al., 2007; IPBES et al., 2016). Demand for pollinator-dependent crops has continued to rise (Aizen et al., 2019) and there is growing international concern over the impact of pollinator losses on food production (IPBES et al., 2016). Within the UK, pollinator populations declined in occupancy by ~25% between 1980 and 2013 (Powney et al., 2019), driven particularly by reduced occurrence of rare species. Declining pollinator populations have been linked with disruptions to plant-pollinator networks (Redhead et al., 2018) and crop pollination deficits have already been recorded (Garratt, Breeze, et al., 2014).

Since the 1930s, the UK's agricultural landscapes have moved from diverse mosaics of mixed farming and semi-natural habitats towards large-scale crop monocultures (Senapathi et al., 2015). These lower complexity landscapes reduce floral resources for pollinators (Baude et al., 2016), resulting in lower pollinator abundance and diversity (Shaw et al., 2020), smaller bumblebee colony size (Bukovinszky et al., 2017) and reduced crop pollinator richness (Fijen et al., 2019). The growth of mass-flowering crops, such as field beans *Vicia faba* and oilseed rape *Brassica napus* (hereafter OSR) can benefit pollinators, by providing highly abundant resources for those physically able to access them (Holzschuh et al., 2013; Westphal et al., 2003). However, their short flowering season rarely covers the entire active period of local pollinators, so life history (whether long-lived and colony building, or solitary and short-lived) affects whether or not corresponding reproductive gains are realised (Riedinger et al., 2015; Westphal et al., 2009).

Furthermore, the practice of crop rotation (whereby arable fields are sown with different crops each year to prevent disease/pest build up and replenish soil nutrients) adds an extra degree of spatiotemporality to these mass-flowering resources, as they are predominantly rotated with cereal crops that offer no resources for local pollinators (Hass et al., 2019; Marja et al., 2018). When mass-flowering crops are absent, local pollinators must therefore endure (often multiple) intervening years of 'resource drought'. Again, individual species' responses to this will be influenced by life history and mobility, with mobile, long-lived pollinators (such as the colony-building *Bombus* sp.) better able to travel and find disparate resources, while more sedentary pollinators (e.g. solitary bees such as *Andrenidae*) will respond more closely to in-situ resource fluctuations (Riedinger et al., 2015).

Fluctuations in pollinator abundance and changes in community composition will have knock-on effects for crop pollination service, which relies on both pollinator abundance and diversity (Garibaldi et al., 2020). Spatial variation in pollinator abundance, due to variable semi-natural habitat provision for pollinators, may cause corresponding variation in the level of pollination service mass-flowering crops receive when rotated between fields, which can, in turn, generate variability in crop yields (Bartomeus et al., 2015; Perrot et al., 2018).

To combat such biodiversity and corresponding ecosystem service declines, agri-environment schemes support growers to increase landscape complexity by either taking land out of production or adding semi-natural habitat along field boundaries (Batáry et al., 2015). Of the boundary measures most commonly supported across Europe, flower-rich field margins and hedgerows are thought to provide the most beneficial resources for pollinators (Cole et al., 2020; Garratt et al., 2017). Both measures can provide floral resources when mass-flowering crops are either absent or not in bloom and for pollinators that cannot utilise mass-flowering crops (Garratt et al., 2017; Grab et al., 2018; Marja et al., 2018). They can also provide important nesting/overwintering sites within arable systems, where much of the land is frequently disturbed and unsuitable (Ullmann et al., 2016), and longer-term studies suggest these measures can genuinely be effective at increasing pollinator populations and pollination services if established for several successive years (Grab et al., 2018; Morandin et al., 2016).

While several studies have demonstrated the benefits of boundary features for pollinator abundance and diversity (e.g. Albrecht et al., 2020; Scheper et al., 2013), less is known about their influence on temporal stability of pollinator abundance and pollination services, partly because field monitoring over long time-scales is challenging. Since consistency of yield is crucial to farmers, increasing attention is being paid to the role of landscape structure in functional stability and crop yield resilience (e.g. Redhead et al., 2020). Floral margins can serve as refuges for pollinators in years of successive cereal crops (Marja et al., 2018) and help sustain pollinators after local crop bloom (Sheffield et al., 2008). Thus, boundary features could stabilise pollinator populations when resources vary temporally across multiple time-scales. This includes resource time-scales shorter than the lifetime of individual pollinators (e.g. weekly, where mass-flowering occurs briefly each year in the same location) and multi-year time-scales longer than the lifetime of individual pollinators (e.g. where resource-rich mass-flowering crops only occur in a given field once in a set number of years). The latter is relevant to the large-scale spatiotemporal dynamics of crop-rotated landscapes.

In this study, we use a validated process-based model to investigate the impacts of boundary features on ground-nesting bee populations under a typical low-diversity rotation cycle and the corresponding level and stability of the pollination service these bees provide for rotated OSR and field bean crops. OSR and field beans are typically included in UK crop rotations in alternating third years following two successive years of cereal production and both can benefit from pollination services (Garratt, Coston, et al., 2014; Lindström et al., 2016; Perrot et al., 2018; but see Bishop et al., 2020). By using computer simulations, we can isolate the influence of crop rotation and estimate impacts over much longer time-scales and larger areas than would ever be feasible with an empirical study. We use a sample of 117 10×10 km^2 study landscapes distributed across England, UK, to represent realistic landscape and boundary feature configurations, and simulate 20 years of crop rotation. Focusing on standard narrow grassy field margins, hedgerows and wide agri-environment margins, we examine how the amount of boundary features in the landscapes affects ground-nesting bee population size and stability (i.e. inter-annual variation in population size). We compare the predicted effects on both mobile, long-lived bumblebees and on sedentary, short-lived solitary bee populations. We then examine how this impacts the level and reliability of crop pollination service, and suggest management approaches for maximising the stabilising effect of field boundary features.

2 | MATERIALS AND METHODS

2.1 | Model description

Poll4pop (Gardner et al., 2020a; developed via Häussler et al., 2017; Lonsdorf et al., 2009; Olsson et al., 2015) is a process-based model that predicts spatially explicit abundance and flower visitation rates by central-place-foraging pollinators (i.e. bees) in a given landscape, based on bee nesting and foraging habitat preferences and typical foraging distances. It can simulate both solitary and social bees (accounting for colony growth over time), allows different ranges for foraging and dispersal, includes preferential use of more rewarding floral and nesting resources, can replicate both floral resource and nest site limitation, and can incorporate fine-scale boundary features in the landscape. By operating on rasterised landscapes, the model can simulate the uneven delivery of pollination service across fields generated by proximity to other habitats.

The model accounts for seasonal differences in the floral cover offered by each habitat and outputs visitation rate per pixel per season, based on the amount of time bees from all nests spend foraging in each pixel. Solitary bees are assumed to be active only during one (user-selected) season, reflecting the short flight periods of the majority of solitary species (Falk, 2015). Social bees (e.g. bumblebees) are assumed to be active across three seasons. The model simulates their colony-building behaviour by assuming queens forage during season 1 to produce workers, which forage during season 2 to produce additional workers. The total resources gathered by all workers during season 3 then determine the number of new queens produced by the nest at the end of the active period. In contrast, the number of new females produced by a solitary bee nest is solely dependent on the resources gathered by the original nest-founding female. The model can be run for multiple years using the dispersed reproductives from the previous year as the starting population for the next and as such can reproduce source/sink population dynamics.

For a detailed description of the model, see Häussler et al. (2017) and for validation of the model in Great Britain (including sensitivity analysis) see Gardner et al. (2020c), henceforth G2020.

2.2 | Model parameterisation

We run the model for ground-nesting bumblebees (e.g. *Bombus terrestris*) and ground-nesting solitary bees (e.g. *Andrenidae*). These are the two largest wild bee guilds in the UK (Falk, 2015) and include many of the key pollinators of OSR and field beans (Hutchinson et al., 2021). We take model parameters for these guilds from G2020. These consist of estimates of nest density and foraging/dispersal distances derived from the literature (Greenleaf et al., 2007; Gathmann & Tscharntke, 2002; Franzén & Nilsson, 2010 as used in Dicks et al., 2015; Häussler et al., 2017), plus estimates of floral cover, foraging attractiveness and nesting attractiveness derived from an expert opinion questionnaire, where experts scored habitats based on their experience (maximum n = 10 UK pollinator experts; see

G2020 for details). We adopt the expert opinion estimates from the G2020 study, rather than the calibrated values, due to the ecological unfeasibility of some of the calibrated values. G2020 showed this model parameterisation incorporating expert opinion estimates produces model predictions that significantly agree with the observed abundances from transect surveys at 239 sites distributed across Great Britain.

To capture the short duration of crop mass-flowering, we adjust the seasonal definitions used in G2020 so that the three seasons for social bees instead represent early spring (roughly March–mid-April; model assumes queens foraging), late spring (mid-April–May; workers foraging) and summer (June–August; workers foraging), where early and late spring each represent half the duration of the final summer season. To reflect this, the original spring floral cover scores for suburban and semi-natural habitats from G2020 are halved and apportioned equally to the new early and late spring seasons (since floral cover within the model represents floral abundance multiplied by duration). Based on the most typical flowering seasons for UK crop types, the original spring floral cover scores for the mass-flowering crops field bean and OSR (and also linseed/flax, peas, strawberries, raspberries and other berries) are assigned to late spring, with zero cover assumed during early spring. The opposite approach is applied to orchards, with their floral cover assigned to early spring. We confirmed that this new seasonal prescription for social bees maintained significant agreement with observed abundances by rerunning the model validation procedure described in G2020 for all 239 sites for bumblebees (see Supporting Information).

For solitary bees, we retained the original spring and summer seasonal definitions used in G2020 (i.e. not subdividing spring into early and late), since solitary bees do not produce workers, typically have shorter flight periods and different species show different emergence times. We run the model twice for solitary bees: once to simulate spring-flying solitary species and once to simulate summer-flying solitary species, where these are assumed independent of the number of spring-flying solitaries, that is, representing different species with later flight periods.

Tables S3 and S4 in the Supporting Information detail the expert-derived floral cover, floral attractiveness and nesting attractiveness parameters used to run the model, representing the resource provision assumed for each landcover class and boundary feature.

2.3 | Study landscapes

We use a sample of 117 10 × 10 km^2 study landscapes (Figure 1), showing wide variation in cereal crop area (interpreted as a proxy for intensity of arable production; Figure 2). These are a subset of the validation landscapes used in G2020, where we now select only those landscapes located within England that contain OSR and field bean fields and that do not significantly overlap with another 10 × 10 km^2 study landscape. Overlapping was permitted in G2020 since the landscapes represented buffers around central survey sites of interest. However, since this study compares landscape-level properties, significantly ($\gtrsim$25%) overlapping landscapes are omitted. Generation of the study landscapes is described fully in the Supporting Information of G2020. Briefly, the landscapes are based on the CEH Landcover Map 2015 (LCM2015), with Ordnance Survey orchard polygons overlaid on top and crop location information for the year 2016 derived from rural payments agency databases. The 10 × 10 km^2 study landscapes are rasterised with 10 × 10 m pixel size.

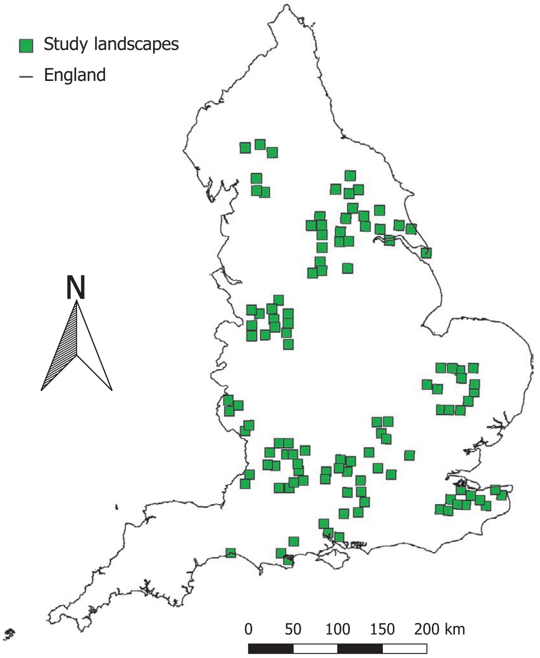


FIGURE 1 Locations of study landscapes within England, UK

2.3.1 | Boundary feature maps

Each landscape is accompanied by three boundary feature maps. The first of these represents hedgerow locations ('hedges') derived from the CEH Woody Linear Features Database (Scholefield et al., 2016), which has been shown to predict abundance of insect species in agricultural landscapes (Sullivan et al., 2017). Since the database does not capture 100% of hedgerows, this is augmented by adding hedgerows around the perimeter of any land parcel claiming for agri-environment hedgerow options through the Countryside Stewardship Scheme in 2016. We assume all hedgerows are 2 m wide (width corresponding to 'favourable condition'; Defra, 2007).

The second boundary feature map represents agri-environment margins ('agri-env.') and incorporates all grassy buffer strips, fallow margins, flower-rich margins and ditches whose presence or management was subsidised during 2016 by the Countryside Stewardship Scheme (see G2020 for a detailed list of the relevant scheme options). A 4 m width is assumed for all these features (since 4–6 m is recommended for buffer strips; e.g. Defra, 2020) and, due to lack of information on the features' exact locations, the features were

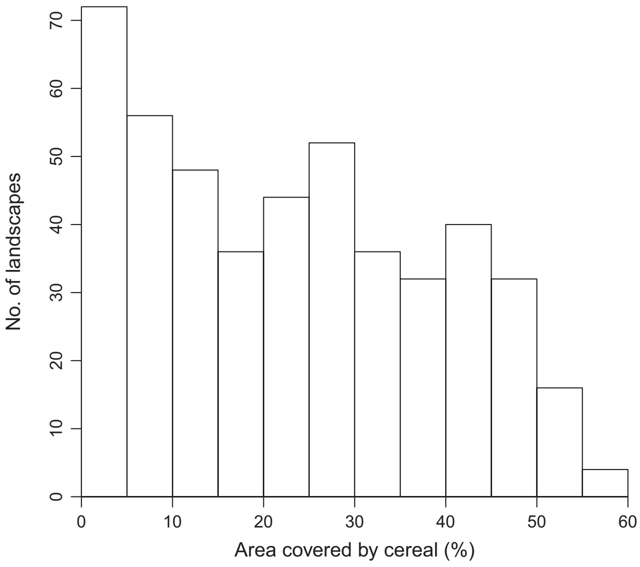


FIGURE 2 Variation in cereal crop area across the 117 10 × 10 km^2 study landscapes

mapped around the entire perimeter of the land parcel associated with the claim. This approximation allows us to identify fields in the landscape with more generous margins, as well as those with fallow areas or enhanced floral resources. The agri-environment margin map is therefore the combination of these wide grassy, fallow and flower-rich margins around specific fields.

The final boundary feature map ('narrow') represents the standard narrow margins around all other fields defined as 'Arable and Horticulture' in LCM2015. These are assumed to be grassy margins 1 m wide.

Each study landscape therefore consists of a base landcover map plus three boundary feature maps ('narrow', 'hedges' and 'agri-env.'), which approximate real-life boundary feature configurations during 2016 and can be added and removed at will. Figure S1 shows how the area of each boundary feature type varies across the 117 study landscapes.

2.4 | Crop rotation sequence

The landcover maps described in §2.3 represent a snapshot of the study landscapes in the year 2016. We impose a 6-year crop rotation sequence of cereal-cereal-OSR-cereal-cereal-field bean and generate crop rotated landscapes for the five subsequent years of this rotation. We note that many of the study landscapes likely undergo a much longer rotation in reality (e.g. with many more consecutive years of cereal), while organic and low input systems often have more variable/diverse rotations. However, we choose a 6-year rotation to facilitate simulation within a reasonable computation time and because shorter rotations are recommended to more sustainably manage soil health/fertility.

Within each landscape, OSR and field bean fields are constrained to be in stages 3 and 6 of the rotation, respectively. However, cereal fields in the original landscape configurations may be in stages 1, 2, 4 or 5. Their progression is not uniquely predetermined by their current state. Therefore, we randomly select a current rotation stage for each cereal field. Since this may influence the results (e.g. if several adjacent fields are randomly assigned the same stage), we simulate 10 alternative realities, where the cereal fields receive an independent random rotation stage allocation in each reality. This allows us to quantify the uncertainty introduced through rotation stage allocation by calculating the mean and standard error across the simulation results from all 10 realities.

2.5 | Boundary feature simulations

We run the model for 20 consecutive years, feeding the number of surviving females from the previous year into the following year and using the crop rotated landscapes described in Section 2.4. This enables us to model three complete cycles of the 6-year rotation sequence, discarding the first year.

We test five scenarios:

1. Base landcover with no boundary features present ('no-boundary-features')
2. Base landcover plus the standard narrow (1 m) grassy margin maps only ('narrow').
3. Base landcover plus the mapped hedges only ('hedges').
4. Base landcover plus the mapped 4 m-wide agri-environment margins only ('agri-env.').
5. Base landcover with all boundary features included ('all features'; see Figure S1 for an indication of the relative areas covered by each boundary feature). Where multiple boundary features occur within a single pixel, the model sums their contributions to the habitat quality accounting for the area that is covered by each boundary feature within the pixel. This scenario represents the real-life boundary feature composition of the landscapes.

For each of the five scenarios, the model is run 10 times for each study landscape—one simulation for each of the 10 random rotation state allocations.

For each simulation, we calculate the total landscape-level visitation rate (i.e. the visitation rate to all pixels within the landscape) in each season in each year, which reflects the total bee population size. We also calculate the total visitation rate to all field bean pixels and the total visitation rate to all OSR pixels in each season in each year.

2.6 | Data analysis

All analyses were conducted using R version 3.5.1 (R Core Team, 2018). For each study landscape, *i*, for each simulation, *j*, for each scenario, *k*, we calculate the time-averaged mean visitation rate ($\text{mean}_{i,j,k}$) across the 20-year period and the root mean square variability about this mean ($\text{rms}_{i,j,k}$), using:

$$\mathrm{rms}_{i,j,k} = \sqrt{\sum_{t=2}^{t=20} (v_{i,j,k}(t) - \mathrm{mean}_{i,j,k})^2}, \quad (1)$$

where $v_{i,j,k}(t)$ is the specified seasonal visitation rate in each year t.

For each study landscape, for each simulation, we then calculate the fractional change in visitation rate ($\delta_{i,j,k}$) between each boundary feature scenario (k = narrow, hedges, agri-env., all) and the scenario with no boundary features present (k = none) using:

$$\delta_{\mathrm{mean},i,j,k} = \frac{(\mathrm{mean}_{i,j,k} - \mathrm{mean}_{i,j,\mathrm{none}})}{\mathrm{mean}_{i,j,\mathrm{none}}}, \quad (2)$$

$$\delta_{\mathrm{rms},i,j,k} = \frac{(\mathrm{rms}_{i,j,k} - \mathrm{rms}_{i,j,\mathrm{none}})}{\mathrm{rms}_{i,j,\mathrm{none}}}. \quad (3)$$

We then average to get the mean fractional change ($\Delta_{i,k}$) over all $N = 10$ simulations for each boundary feature scenario in each landscape and its standard error ($\alpha_{\Delta_{i,k}}$) using:

$$\Delta_{\mathrm{mean},i,k} = \frac{\sum_{j=1}^{j=10} \delta_{\mathrm{mean},i,j,k}}{N}, \quad (4)$$

$$\alpha_{\Delta_{\mathrm{mean},i,k}} = \sqrt{\frac{\sum_{j=1}^{j=10} (\delta_{\mathrm{mean},i,j,k} - \Delta_{\mathrm{mean},i,k})^2}{N(N-1)}}, \quad (5)$$

$$\Delta_{\mathrm{rms},i,k} = \frac{\sum_{j=1}^{j=10} \delta_{\mathrm{rms},i,j,k}}{N}, \quad (6)$$

$$\alpha_{\Delta_{\mathrm{rms},i,k}} = \sqrt{\frac{\sum_{j=1}^{j=10} (\delta_{\mathrm{rms},i,j,k} - \Delta_{\mathrm{rms},i,k})^2}{N(N-1)}}. \quad (7)$$

For each boundary feature scenario (k = narrow, hedges, agri-env., all), we assess how the fractional change in time-averaged mean visitation rate and the fractional change in rms variability depend on boundary-feature area within the landscape ($A_{i,k}$; units = m^2) by fitting the linear models:

$$\Delta_{\mathrm{mean},i,k} = \beta A_{i,k} + \gamma(\mathrm{mean}_{i,\mathrm{none}}) + \eta(\mathrm{rms}_{i,\mathrm{none}}) + \kappa A_{\mathrm{cereal}} + \varepsilon_{i,k}, \quad (8)$$

$$\Delta_{\mathrm{rms},i,k} = \beta A_{i,k} + \gamma(\mathrm{mean}_{i,\mathrm{none}}) + \eta(\mathrm{rms}_{i,\mathrm{none}}) + \kappa A_{\mathrm{cereal}} + \varepsilon_{i,k}, \quad (9)$$

where β, γ, η and κ are fitted coefficients; $\varepsilon_{i,k}$ is a Gaussian-distributed error term; $\mathrm{mean}_{i,\mathrm{none}}$ and $\mathrm{rms}_{i,\mathrm{none}}$ are the simulation-averaged, time-averaged mean visitation rate and visitation rate rms for the landscape with no boundary features present; and A_{cereal} is the area of cereal within the landscape. A_{cereal} controls for the fact that landscapes with a smaller area of rotatable crops will have less variable bee populations in our prescription where crop rotation is the only source of variability. The contribution of each $\Delta_{\mathrm{mean},i,k}$ and $\Delta_{\mathrm{rms},i,k}$ to the fit is weighted by the inverse of its standard error.

The magnitude and significance of the fitted coefficient β therefore allow us to compare how the fractional change in time-averaged mean visitation rate (or rms variability in visitation rate) relative to the no-boundary features value depends on the area within the landscape covered by that boundary feature.

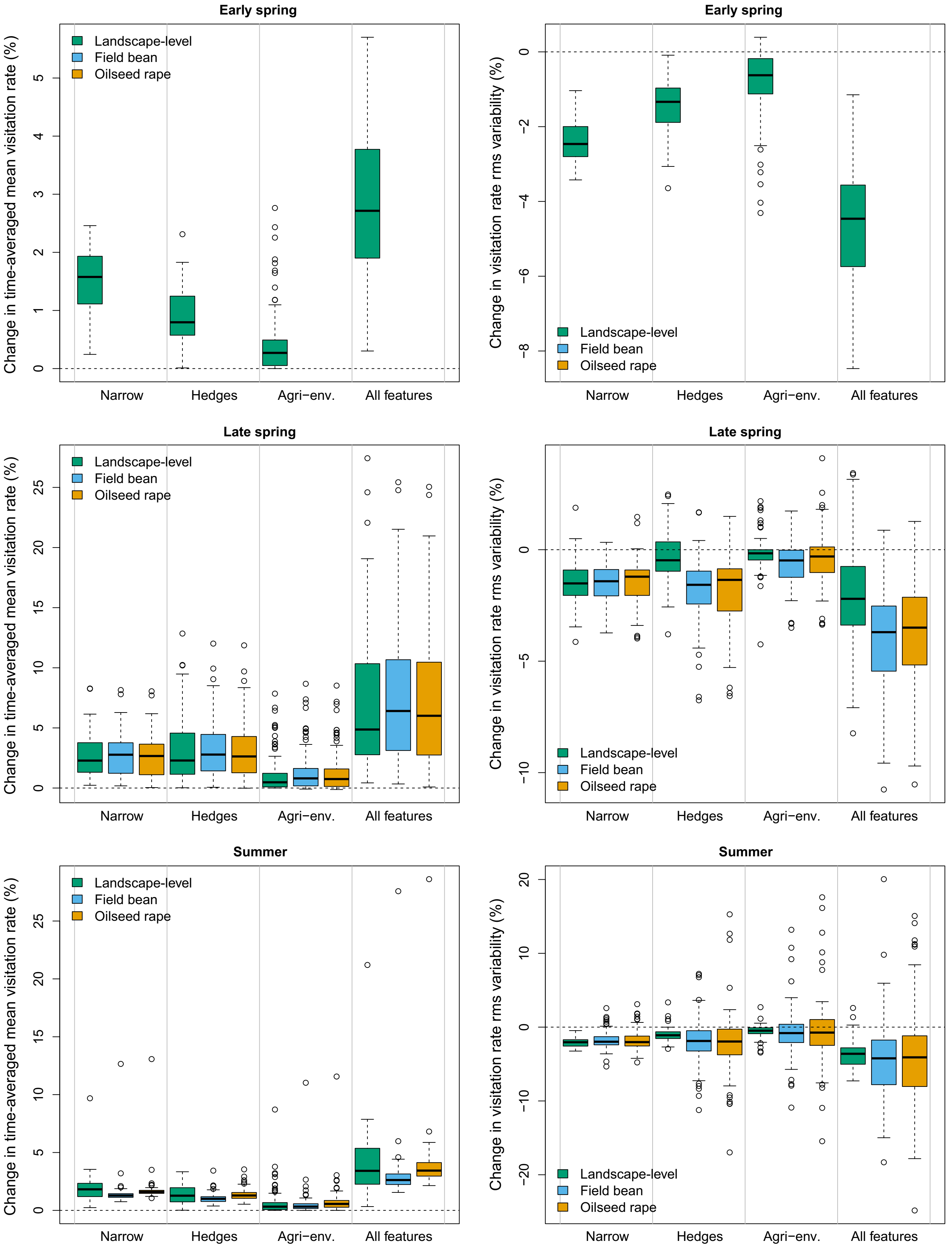
3 | RESULTS

3.1 | Ground-nesting bumblebees

When boundary features were included in the simulations, the landscapes typically showed higher bumblebee visitation rates (at landscape-level and in-crop) that were more stable over time (i.e. higher mean and lower rms variability). Across all landscapes, the median increase in time-averaged mean visitation and reduction in variability when all boundary feature types were included was between ~3% and 5%, but was as large as 20%–25% in some of the most arable landscapes (Figure 3). Including the standard narrow margins or hedges generally produced a larger change than including the agri-environment margins, suggesting the former made the largest contribution to the total effect in these landscapes. This reflects the fact that, although the agri-environment margins were wider than the other boundary features, only a small number of fields within the landscapes contained them so that the total area of these features in the study landscapes was typically small (Figure S1).

The wide range in $\Delta_{\mathrm{mean},i,k}$ and $\Delta_{\mathrm{rms},i,k}$ values shown in Figure 3 reflects the fact that both boundary-feature area and rotating-crop area varied across the landscapes. Fitting Equations 8 and 9 allowed us to separate these effects and isolate the relative effect per unit area of each type of boundary feature. This demonstrated that landscapes with a greater area of boundary features showed higher time-averaged mean landscape-level bumblebee visitation rates (i.e. larger bumblebee populations) relative to the no-boundary-features scenario (Figure 4, left-hand plots, green bars). This was true for all seasons. The agri-environment margins produced the greatest fractional change in mean visitation rate per unit area, likely due to these features providing a combination of nesting and floral resources often clustered together in nearby fields collectively managed by a single participating farm. In the all-boundary-features scenario, the fractional change in mean visitation rate per unit area was intermediate between the standard narrow margins and hedge only scenarios, despite including all boundary features. This is due to these more common boundary features covering a far greater area within the

FIGURE 3 Change in ground-nesting bumblebee landscape-level, field bean and OSR visitation rates for each boundary feature scenario, relative to the no-boundary-features scenario, for the 117 study landscapes. Left-hand panels show percentage change in the mean visitation rate across the 20-year simulation ($100 \times \Delta_{\mathrm{mean}}$). Right-hand panels show percentage change in visitation rate variability over time ($100 \times \Delta_{\mathrm{rms}}$). Panels from top to bottom show early-spring (no field bean/OSR flowering), late-spring and summer visitation rates, respectively


Early spring
Late spring
Summer
Change in time-averaged mean visitation rate (%)
Change in visitation rate rms variability (%)
🟩 Landscape-level
🟦 Field bean
🟧 Oilseed rape
Narrow
Hedges
Agri−env.
All features
0
1
2
3
4
5
0
−2
−4
−6
−8
0
5
10
15
20
25
0
−5
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−20

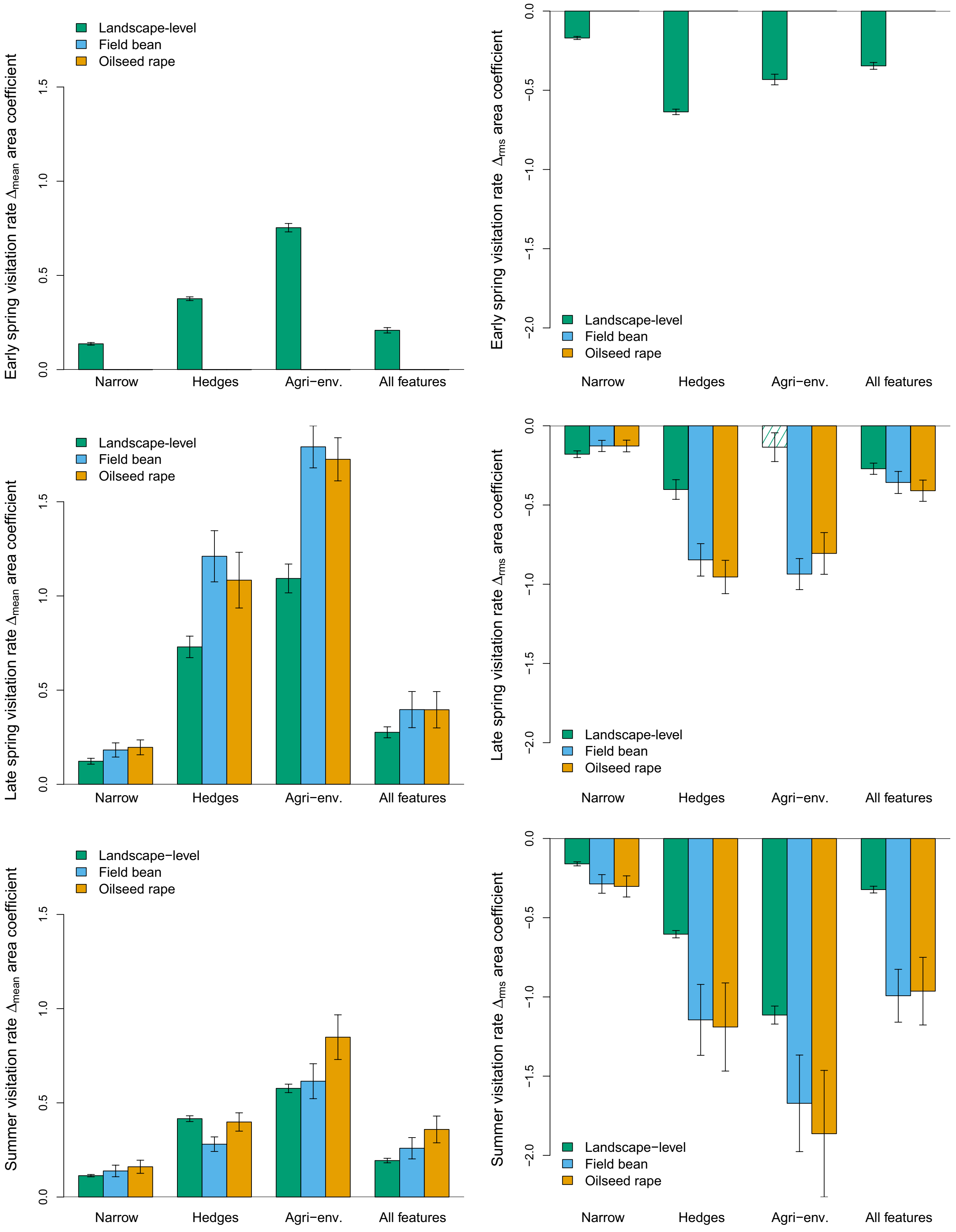
Early spring visitation rate Δ_{mean} area coefficient
Early spring visitation rate Δ_{rms} area coefficient
Late spring visitation rate Δ_{mean} area coefficient
Late spring visitation rate Δ_{rms} area coefficient
Summer visitation rate Δ_{mean} area coefficient
Summer visitation rate Δ_{rms} area coefficient
Landscape-level
Field bean
Oilseed rape
Narrow
Hedges
Agri−env.
All features
0.0
0.5
1.0
1.5
−0.5
−1.0
−1.5
−2.0

FIGURE 4 Dependence of fractional change in ground-nesting bumblebee visitation rate on boundary-feature area, where the fractional change is calculated relative to the no-boundary-features scenario and bar heights represent area coefficients for landscape-level (green), field bean (blue) and OSR (orange) visitation rates, respectively. Left-hand panels correspond to fractional change in mean visitation rate across the 20-year simulation. Right-hand panels correspond to fractional change in visitation rate variability over time (rms). Panels from top to bottom show early-spring (no field bean/OSR flowering), late-spring and summer visitation rates, respectively. Solid bars indicate area coefficients that are statistically significantly different from zero; hatched bars indicate no statistically significant difference from zero. Error bars show standard error

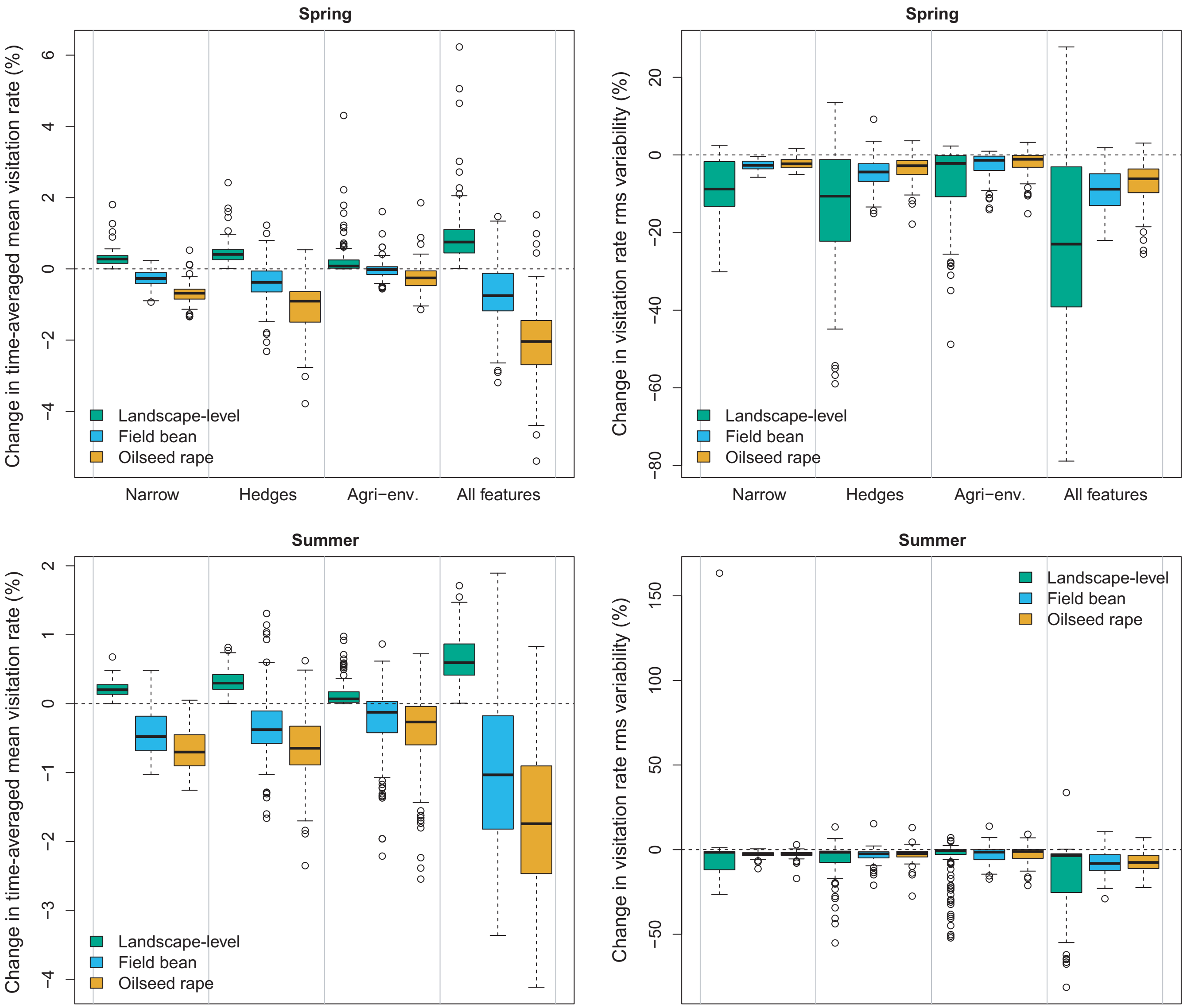

FIGURE 5 Change in ground-nesting solitary bee landscape-level, field bean and OSR visitation rates for each boundary feature scenario, relative to the no-boundary-features scenario, for the 117 study landscapes. Left-hand panels show percentage change in the mean visitation rate across the 20-year simulation ($100 \times \Delta_{\text{mean}}$). Right-hand panels show percentage change in visitation rate variability over time ($100 \times \Delta_{\text{rms}}$). Top and bottom panels show spring and summer visitation rates, respectively

study landscapes than the agri-environment margins (Figure S1) and so dominating the overall landscape response.

The seasonal landscape-level bumblebee visitation rates were also more stable relative to the no-boundary-features scenario in landscapes with a greater area of boundary features (Figure 4, right-hand plots, green bars). In early spring, hedgerows provided the strongest stabilising effect, that is, most negative $\Delta_{\text{rms},i,k}$ coefficient, indicating a ~7% reduction in rms variability per unit increase

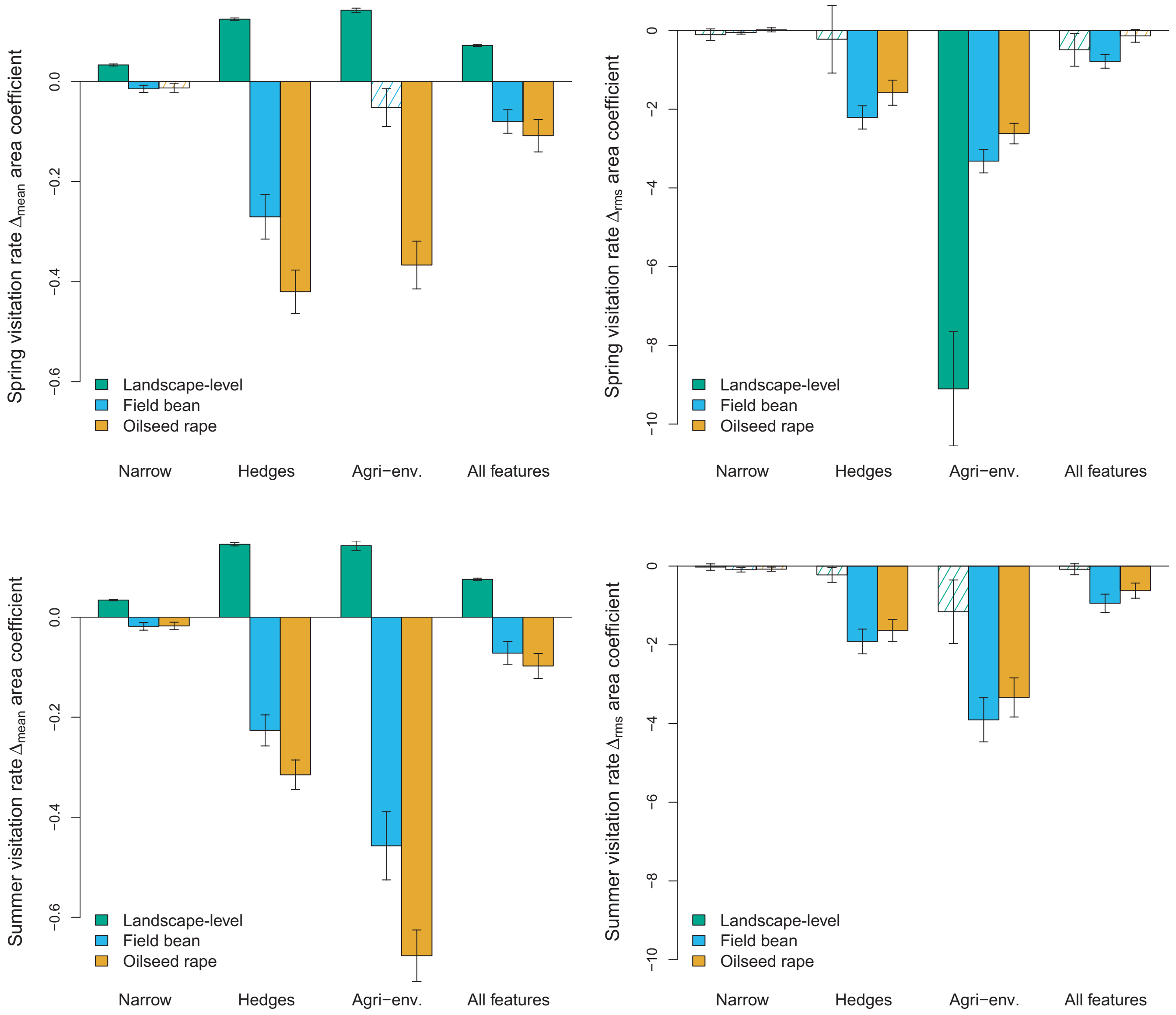

FIGURE 6 Dependence of fractional change in ground-nesting solitary bee visitation rate on boundary-feature area, where the fractional change is calculated relative to the no-boundary-features scenario and bar heights represent area coefficients for landscape-level (green), field bean (blue) and OSR (orange) visitation rates, respectively. Left-hand panels correspond to fractional change in mean visitation rate across the 20 year simulation. Right-hand panels correspond to fractional change in visitation rate variability over time (rms). Top and bottom panels show spring and summer visitation rates, respectively. Solid bars indicate area coefficients that are statistically significantly different from zero; hatched bars indicate no statistically significant difference from zero. Error bars show standard error

in hedgerow area. In late spring, during mass crop flowering, agri-environment margins provided no statistically significant stabilising effect on bumblebee landscape-level visitation (likely due to their small total area within each study landscape with respect to the flowering crops) but they did provide the largest (and a statistically significant) stabilising effect in summer (~12% rms variability reduction per unit area).

The in-crop bumblebee visitation rate showed similar trends to the landscape-level visitation (Figure 4; blue and orange bars). Landscapes with a greater area of boundary features showed significantly higher time-averaged field bean and OSR visitation rates (>10% higher per unit area of hedges or agri-environment margins during peak late-spring flowering) and significantly more stable field bean and OSR visitation rates (~8% more stable per unit area for the same boundary features and season) with respect to the no-boundary-features scenario. In many cases, the effect per unit area of boundary feature was stronger for in-crop bumblebee visitation rates than at landscape-level, due to the in-crop visitation including less dilution from stable sub-populations based in non-crop landcovers remote from agricultural boundary features.

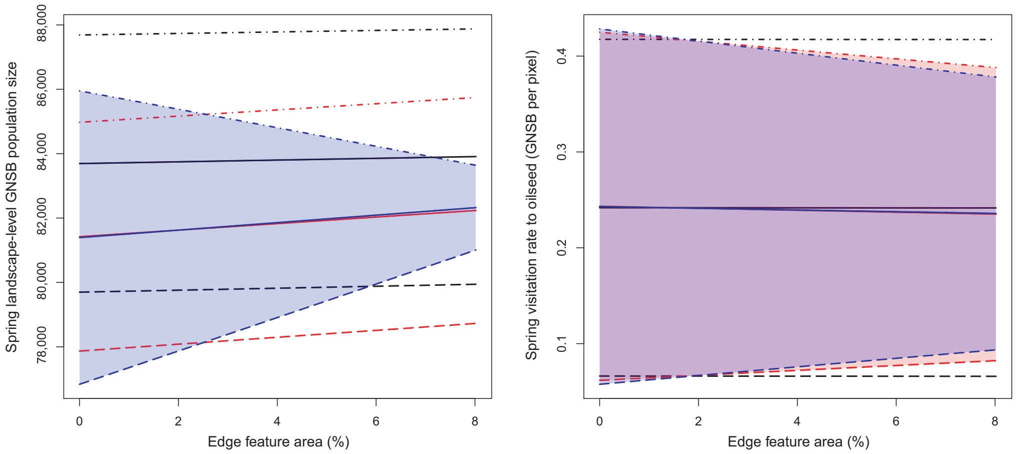

FIGURE 7 Predicted ground-nesting solitary bee landscape-level population (left) and OSR visitation rate (right) trends with increasing boundary-feature area for a highly arable study landscapes (cereal fraction = 54.4%). Trends are calculated using Equations 8 and 9, the fitted coefficients from Figure 6 and dependent variable values specific to the study site. The maximum boundary-feature area shown corresponds to the maximum arable boundary area of the study site with its current field sizes. Black, red and blue lines show the predicted trends for standard narrow margins, hedges and wide agri-environment margins, respectively. Solid lines show the time-averaged mean level, dashed lines show mean-rms and dot-dashed lines show mean + rms. Shading between these indicates a significant reduction in predicted rms variability around this mean with increasing boundary-feature area

3.2 | Ground-nesting solitary bees

For solitary bees, when boundary features were included in the simulations, the landscapes typically showed higher landscape-level visitation rates that were more stable over time. Although the increase in mean landscape-level visitation was generally small (<1%), the reduction in landscape-level variability when all boundary features were included was as large 80% in some landscapes, with median reductions of ~20% and ~5% during spring and summer, respectively (Figure 5, green boxes). The in-crop field bean and OSR solitary bee visitation rates were also typically more stable over time (median values of ~5%–10% across all landscapes for the 'all features' scenario), but the time-averaged mean visitation rates to these crops were generally lower, with median values indicating 1%–2% reductions for the 'all features' scenario (Figure 5, blue and orange boxes).

Fitting Equation 8 confirmed that landscapes with a greater area of boundary features showed significantly higher time-averaged landscape-level solitary bee visitation rates (i.e. larger solitary bee populations) relative to the no-boundary-features scenario (Figure 6, left-hand plots, green bars). This was true in both spring and summer. However, there was no significant trend in landscape-level solitary bee visitation rate rms variability with increasing boundary-feature area, despite solitary bee populations on average being more stable when boundary features were present in the landscapes as opposed to absent (compare Figures 6 and 5, right-hand plots, green bars/boxes). An exception was the agri-environment margins scenario in spring, which did show a landscape-level stabilising effect that significantly increased with increasing area of agri-environment margins; this indicated a potential ~900% reduction in landscape-level rms variability per unit area of agri-environment margins, for our particular model assumptions. Figure 7 (left panel) shows the predicted strength of this stabilising effect on the landscape-level solitary bee population in one of the highly arable study landscapes, illustrating the predicted increase in time-averaged mean and decrease in variability amplitude as a function of agri-environment margin cover within the landscape.

The fits also confirmed that landscapes with a greater area of boundary features are predicted by the model to show a lower time-averaged mean solitary bee visitation rate to field bean and OSR compared to the no-boundary-features scenario (Figure 6; blue and orange bars). Although the standard narrow margins scenario does not show any significant decrease in $\Delta_{\mathrm{rms},i,k}$ with increasing area, the other boundary feature scenarios do (with the exception of the spring all-boundary-features scenario), confirming an increase in boundary-feature area significantly decreases solitary bee in-crop visitation rate rms variability in these cases (Figure 6, right-hand plots, blue and orange bars). Figure 7 (right-hand panel) illustrates how this decrease in variability amplitude can compensate for the small reduction in time-averaged mean visitation rate such that the expected minimum yearly crop visitation rate (mean-rms) is nonetheless higher in the scenario with boundary features present than without.

4 | DISCUSSION

This study used a validated process-based model and 117 study landscapes in England to explore the impacts of boundary features (hedgerows and field margins) on the stability of ground-nesting bee populations and their associated pollination service under common UK crop rotations. The use of simulations enabled us to assess potential impacts without interference from other sources of variability (e.g. weather) and across longer times-scales and more landscapes than would ever be feasible with an empirical study. Our findings demonstrate the stabilising effect these features can have upon populations and pollination services by buffering them against the spatially and temporally variable resources generated by low-diversity crop rotations.

4.1 | Impacts of boundary features on bee population stability

According to the simulations, ground-nesting bumblebees show larger and more stable populations when boundary features are present and this effect increases with increasing boundary-feature area within the landscape. The relative importance of different boundary features for stabilising bumblebee populations varies seasonally according to their nesting and floral resources. During spring, hedgerows provide the largest stabilising effect due to their high nesting attractiveness and high spring floral cover scores, which represent the early floral resources provided by blackthorn *Prunus spinosa* and later hawthorn *Crataegus monogyna*. In summer, agri-environment margins are predicted to be the most stabilising, due to the later flowering period of many common flower-rich mixes (Byrne & delBarco-Trillo, 2019; Cole et al., 2020; but see Timberlake et al., 2019). The seasonal importance of different boundary features for promoting stability reflects the bumblebees' requirement for sustained floral resources throughout the prolonged lifetime of the colony and emphasises the importance of multiple boundary features if a single feature cannot provide continuous resources (which most do not; Cole et al., 2020), providing at least one feature also provides nesting resources.

For ground-nesting solitary bees, the simulations show that boundary features likewise increase populations, but only wide agri-environment interventions provide any significant stabilising effect and only during spring. This is due to their shorter lifetimes, lack of colony building behaviour and shorter foraging/dispersal distances. In most species, a solitary bee female provisions her own nest and the offspring emerge the following year. Other more complex/bivoltine life histories exist for some species (e.g. *Andrena trimmerana*; Falk, 2015), but these are not simulated by the model, which assumes independent spring-flying and summer-flying solitary bee populations. Consequently, the simulated solitary bee populations increase with the nesting opportunities the boundary features offer, but their productivity is still strongly influenced by immediate floral resources during their short foraging window, which includes the variable resources from nearby rotated crops. As such, for solitary bees, boundary features do not generate the more extensive stabilising influence experienced by the longer-lifetime bumblebees. Furthermore, the shorter foraging/dispersal distances of solitary bees (~100–200 m vs. 500–1,000 m for bumblebees; Carvell et al., 2012; Gathmann & Tscharntke, 2002) increase their reliance upon permanently concurrent patches of good floral and nesting resources and they cannot take advantage of boundary features to effectively shift their population centre in pursuit of the rotating mass-flowering crops like the more mobile bumblebees. Thus, while boundary features can boost the solitary bee population, larger permanent semi-natural habitat patches within agricultural settings will be more effective for maintaining landscape-level solitary bee population stability, providing these patches contain good nesting resources and sufficient phenologically concurrent floral resources to self-sustain the solitary bee population within the habitat patch, without resorting to resources beyond it.

Many studies suggest that interventions are most effective in low–moderate complexity landscapes, where the ecological contrast is greatest (Grab et al., 2017; Tscharntke et al., 2005). Our comparisons of bumblebees and solitary bees indicate that these concepts of complexity and effectiveness are dependent on the spatial scale at which the species operates and how this relates to the size of and spacing between interventions, especially when population stability is considered in addition to population size. We note our simulations assumed fixed locations for the agri-environment features. If the features are rotated between years (e.g. Defra, 2020), their predicted stabilising effect could be diminished if overwintering sites are destroyed in the process, or potentially enhanced if deliberately placed to counter mass-flowering crop availability.

Although the median predicted changes in population abundance and stability are generally small across our simulated landscapes (<10%), we stress these are the net changes measured at the $10 \times 10\ \mathrm{km}^2$ landscape scale and incorporate dilution by stable populations in unchanging habitats distant from both rotating crops and boundary features. Our model's foraging prescription replicates the diminishing impact of boundary features on pollinator abundance with distance observed in the field (MacInnis et al., 2020; Morandin & Kremen, 2013), implying that more extreme changes would have been recorded had we chosen to measure over smaller spatial scales and that increasing the landscape-level effect would require increasing boundary feature cover beyond current levels.

Boundary features can provide additional benefits to bumblebee and solitary bee population size and stability beyond those captured by our simulations. First, primitively eusocial/bivoltine solitary bee species, which were not modelled, may benefit from the longer-term resource availability provided by boundary features in a similar manner to bumblebees, potentially experiencing a greater stabilising effect than demonstrated by our simulations for single-brood solitary bees. Second, we have used general floral attractiveness scores for bumblebees and solitary bees that assume both guilds are able to make some use of mass-flowering crop resources. Species within these guilds not physically able to access these resources (e.g. due to flower morphology) will potentially experience even greater benefits from increasing alternative habitat via boundary features. Third, although sophisticated and capable of reproducing observed bee abundances (G2020), our model does not include the movement of males or the explicit movement paths and mortality of dispersing females beyond their inability to find a suitable nest site. Instead, a standard dispersal distance is assumed independent of landscape context. This may be a reasonable assumption for strongly philopatric solitary bees, but may not be for bumblebees with longer-dispersal distances (Redhead et al., 2016). If males and dispersing queens are less likely to successfully cross open post-harvest fields, semi-natural boundary features may provide bumblebees with crucial pathways for genetic exchange, as well as resources to sustain dispersing females. Understanding these core aspects of species' ecology and incorporating explicit sub-models of this movement process (e.g. similar to those developed for butterflies; Evans et al., 2019) would allow improved estimates of the importance of boundary features for different bee species.

4.2 | Impacts of boundary features upon the stability of crop pollination services

Examining the predicted visitation rates to field bean and OSR showed that the larger, more stable bumblebee populations produced by increasing boundary features translated directly into significantly larger and more stable pollination service from bumblebees to these mass-flowering crops. In the model, the early-spring-foraging queens gather more resources when boundary features are present, producing larger numbers of workers to forage on the late-spring flowering crops. The trends imply that if standard 1 m grassy field margins were replaced by wider 4 m agri-environment margins with their enhanced floral and nesting resources, then the stabilising effect on crop visitation from bumblebees would be up to 10 times stronger per unit area of boundary feature. However, these effects may take some years to become fully established in reality (Morandin et al., 2016) and would depend on the quality of the boundary feature (e.g. Garratt et al., 2017).

In contrast, the simulations predict that boundary features slightly reduce crop visitation from solitary bees, despite increasing the landscape-level solitary bee population. Solitary bees do not produce workers, so although there are more foraging females, these are now sharing their foraging time between the boundary features and the crops, so pollination service to crops is lower (as also predicted by Nicholson et al., 2019). However, for many landscapes, the pollination service that is provided by solitary bees is significantly more stable, with a higher minimum visitation rate when boundary features are present (Figure 7), despite the lower time-averaged mean delivery. Consequently, individual years/fields may be less likely to fall below thresholds for optimal pollination service and yields may be more consistent.

Kremen et al. (2004) presented empirical evidence of increased crop pollination service stability over time with increasing semi-natural habitat, although their measurements related to service stability over the course of a single year. In contrast, Pywell et al. (2015) measured pollinator abundance and crop yield over a 5-year rotation sequence across fields with different proportions of wildlife habitat, demonstrating a higher proportion of such habitat resulted in higher yields per unit area (when averaged over the rotation sequence). However, effects on inter-annual variability amplitude could not be investigated due to continued yield increases throughout the lifetime of the study. Nonetheless, their measured 35% increase in field bean yield with 8% of cropland dedicated to wildlife habitat suggests greater benefits may be realised than predicted by our study.

Again, we note boundary features are likely to produce additional crop pollination service benefits beyond those captured by our simulations. Primitively eusocial/bivoltine solitary bee species, which were not modelled, may show increases in crop visitation more similar to bumblebees than the single-brood solitary bees. Our guild-level model also does not capture the fact that boundary features can promote a more diverse solitary bee community (Sheffield et al., 2008). This benefits crop pollination service because the short flight periods of many solitary bee species, and the influence of weather on both bee and plant phenology, can easily cause mismatches between crop flowering and solitary bee emergence. A more diverse solitary bee community with a variety of emergence times increases the likelihood that crop flowering occurs within the flight period of at least one solitary species each year, regardless of when the crop flowers.

4.3 | Management implications

4.3.1 | Yield stabilisation

Although the benefits of pollination services to arable crops are modulated by a number of factors, such as variety and growing conditions (Bartomeus et al., 2015; Bishop et al., 2020), consistent availability of pollination service is likely to have a stabilising effect on yield, resulting in more consistent harvests over time. This could have significant economic benefits to growers in countries such as the UK that are vulnerable to pollinator declines (Aizen et al., 2019), particularly in the case of field beans, which rely upon bumblebees for pollination (Garratt, Coston, et al., 2014; but see Kirchweger et al., 2020). As farmers are often risk averse, emphasising these yield-stabilising benefits could help incentivise farmers to proactively increase the area and quality of boundary features (IPBES et al., 2016).

4.3.2 | Timing of crop sowing/flowering

The predicted stabilising benefits for bumblebee crop pollination service were greater later in the year (Figure 4), due to the accumulative stabilising effects of earlier seasons (as has been observed in real systems; Grab et al., 2017; Riedinger et al., 2014). Our study used floral cover scores for OSR reflective of autumn-sowing (i.e. peak flowering in late spring; Table S3). However, the results suggest later flowering, spring-sown OSR (and field bean), would potentially receive the most stable pollination service, providing sufficient spring-flowering boundary features build up the bee population prior to crop flowering. Maximal benefits would likely be achieved if rotations can permit autumn-sown and spring-sown mass-flowering crops to be grown in close proximity such that early-spring-flowering boundary features encourage bumblebee queens to found nests ready for the late-spring-flowering crop, which, in turn, increases the number of workers for pollinating the summer-flowering crop.

4.3.3 | Crop rotation sequence

Our 6-year rotation assumption likely exaggerated spatiotemporal resource variation in landscapes where rotations are typically much longer and include more consecutive years of cereal (e.g. eastern England). Under longer, more cereal-dominated rotations, we expect lower bee abundance (due to less floral resources at landscape-level; Marja et al., 2018) and lower intrinsic population variability (due to less crop variation), making boundary features more important for simply sustaining base population levels in such systems, rather than reducing variability. As rotation sequences shorten and the proportion of mass-flowering crops in the landscape increases (approaching our tested 6-year rotation), the stabilising role of boundary features on pollinators and pollination service will become progressively more important.

For simplicity, we did not include maize or grass ley within our tested rotation sequence, which are often incorporated in livestock-dominated areas (e.g. western England). Maize is relatively resource poor for ground-nesting bees (Table S4; Hass et al., 2019), so its function within a rotation would be similar to other cereals. Grass leys are similarly resource poor, unless florally enhanced, for example, with clover/legumes (Holland et al., 2015), in which case they can contribute towards landscape-level availability/consistency of floral resources within rotational systems (Carrié et al., 2018).

4.3.4 | Lockstepping

Farmers often manage fields in lockstep, growing the same crop in adjacent fields to allow efficient use of machinery. This effectively increases the spatial scale at which crops are rotated, making it harder for bees surrounded by lock-stepped cereal fields to forage in and disperse to more distant mass-flowering crop fields. The shorter the foraging/dispersal range of the bee, the more its population will suffer from large field sizes and lockstepping practices. Our simulations assumed that the rotation stage of a field is independent of adjacent fields. Where lockstepping is practised, boundary features will be even more important to help maintain and stabilise bee populations.

4.3.5 | Boundary feature management

We assumed constant habitat quality over time for the boundary features in our simulations. However, most features require periodic management (every ~3 years) to maintain floral diversity (in the case of flower margins) or for general maintenance (in the case of hedgerows). Synchronising boundary feature management with crop rotation could extend their stabilising benefits for pollinator populations and pollination service beyond those captured by our simulations, through (a) timing feature management to ensure sufficient floral resources remain when mass-flowering crops are absent from a field, and (b) scheduling the peak habitat quality of features to encourage the more mobile bumblebee populations to follow rotated mass-flowering crops around the farmscape. If crops are rotated through adjacent fields, late-summer-flowering boundary features could be used to sustain and direct dispersing bumblebee reproductives towards the next fields allocated for mass-flowering crops. Since newly emerged queens searching for nests in early spring will preferentially choose locations close to current floral resources, early-flowering boundary features could then be used to encourage them to nest in those fields. Hedgerows often provide the most abundant early spring floral resources (e.g. via blackthorn *Prunus spinosa*) so this suggests avoiding cutting hedgerows the year before planting a mass-flowering pollinator-dependent crop, since flowering can be significantly reduced post-cutting (Staley et al., 2012). This will ensure the hedgerow supplies maximum early-spring floral resources and builds up a larger bee population in preparation for crop flowering. When pollinator-dependent crops are absent from a field, only cutting half of the hedgerow in any given year would ensure some resources remain to sustain the infield bee population and we recommend future agri-environment schemes support such half-hedge cutting approaches (in addition to the reduced 3-year cutting regime already supported by many schemes) to encourage adoption of this practice despite the practical disincentives.

The projected benefits of boundary features could be further enhanced by tailoring their floral composition, flowering phenology and nest site provision to better fit the needs of the local pollinator community. Presently, many existing margins supported by agri-environment schemes do not provide the breadth of resources necessary to support rare or specialised pollinator communities (Wood et al., 2015) that often act as locally important pollinators (Hutchinson et al., 2021). Ensuring high nesting and floral trait diversity in boundary features will promote bee species richness as well as abundance, by providing niches for previously excluded species and reducing competition (Diekötter et al., 2010).

4.3.6 | Accounting for other sources of variability

Our simulations focused entirely on pollinator population variability induced through crop rotation. However, pollinators show large population fluctuations in response to weather patterns, which are expected to become less consistent under climate change (Kerr et al., 2015; Schürch et al., 2016). Maintaining complex boundary features, which include variation in aspect and vegetation structure and so provide a variety of stable microclimatic conditions, may help buffer populations against weather extremes and so potentially help to mitigate both weather-induced variability and variability generated via spatially/temporally unpredictable crop flowering.

Pesticide regimes represent another potential driver of spatial and temporal pollinator population variability (Brittain et al., 2010). Again, maintaining wide boundary features, which allow distancing of floral resources from crop spray drift, may reduce negative effects (Stuligross & Williams, 2020; but see Main et al., 2020; Main et al., 2020).

5 | CONCLUSIONS AND RECOMMENDATIONS

Crop rotation is necessary, and may become increasingly important in the drive to reduce external inputs in agriculture, but it can add an extra stressor to pollinator populations in terms of resources dynamics, especially when field sizes are large. Field boundary features offer a way to mitigate this and still maintain substantial, stable and resilient pollinator populations and pollination service to pollinator-dependent crops undergoing rotation. They increase nesting resources and provide a continuity of floral resources that bolsters populations in the face of temporally constrained or absent mass-flowering crops. They also offer an opportunity to dedicate land to buffering these pollinator populations and their crop pollination service against climate change impacts, by providing a succession of floral resources to support multi-species populations and guard against phenological mismatches between pollinator activity and crop flowering.

Motivated by our simulations, we summarise below our recommendations for using field boundary features to promote stability of bee populations and pollination service in rotational systems:

1. **Combinations of boundary features**. Maximum benefit is likely to be achieved by combining multiple boundary features (hedgerows, grassy margins and flower-rich margins), since different boundary features provide benefits in different seasons. Ensure chosen boundary feature combinations provide good quality nesting resources within foraging range (<500 m) of a succession of complimentary and abundant floral resources of diverse floral morphologies (see e.g. Nowakowski & Pywell, 2016).
2. **Larger permanent patches of semi-natural habitat, for example, permanent wide (4 m) margins, are necessary for stabilising less mobile solitary bee populations**. Solitary bees have faster life histories, shorter foraging range and often have strong philopatry (particularly in species with specialised soil requirements for nesting), so narrow margin approaches are not as effective for stabilising their populations under crop rotation as they are for stabilising the more mobile bumblebees. Therefore, dedicate larger permanent semi-natural habitat patches to maintaining strong solitary bee populations and let the crops come to them.
3. **Synchronise boundary feature management with crop rotation and rotate mass-flowering crops sequentially through adjacent fields, where possible**. This will maintain resources for infield bee populations when mass-flowering crops are absent and will better enable populations of more mobile species to follow mass-flowering crops, especially if guided by provision of overwintering sites and early floral resources.
4. **Increase boundary-feature area and reduce distance between boundary features (i.e. reduce field sizes), where possible**. The stabilising benefit of boundary features on bee populations will be optimised where boundary features are spaced within the typical dispersal distance (200–1,800 m, depending on species). The stabilising benefit of boundary features on pollination service will be optimised where boundary features providing nesting and sustained floral resources occur within the typical foraging range (100–500 m) of pollinator-dependent crops.

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AUTHORS' CONTRIBUTIONS

E.G. devised and carried out the research; E.G. wrote the manuscript with contributions from T.D.B.; Y.C. provided poll4pop pollinator model. All other authors provided comments on the manuscript and/or datasets for model validation.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.9cnp5hqfw (Gardner et al., 2020b). Process-based pollinator model freely available to download from https://github.com/yclough/poll4pop (https://doi.org/10.5281/zenodo.4001015; Gardner et al., 2020a).

ORCID

Emma Gardner https://orcid.org/0000-0002-1669-7151
Tom D. Breeze https://orcid.org/0000-0002-8929-8354
Yann Clough https://orcid.org/0000-0002-2901-7602
Michael P. D. Garratt https://orcid.org/0000-0002-0196-6013
Deepa Senapathi https://orcid.org/0000-0002-8883-1583
Duncan B. Westbury https://orcid.org/0000-0001-7094-0362

REFERENCES

Aizen, M. A., Aguiar, S., Biesmeijer, J. C., Garibaldi, L. A., Inouye, D. W., Jung, C., Martins, D. J., Medel, R., Morales, C. L., Ngo, H., Pauw, A., Paxton, R. J., Sáez, A., & Seymour, C. L. (2019). Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Global Change Biology*, *25*(10), 3516–3527.

Albrecht, M., Kleijn, D., Williams, N. M., Tschumi, M., Blaauw, B. R., Bommarco, R., Campbell, A. J., Dainese, M., Drummond, F. A., Entling, M. H., Ganser, D., de Groot, G. A., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., … Sutter, L. (2020). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: A quantitative synthesis. *Ecology Letters*, *23*(10), 1488–1498.

Bartomeus, I., Gagic, V., & Bommarco, R. (2015). Pollinators, pests and soil properties interactively shape oilseed rape yield. *Basic and Applied Ecology*, *16*(8), 737–745.

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, *29*(4), 1006–1016.

Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., & Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, *530*(7588), 85–88.

Bishop, J., Garratt, M. P. D., & Breeze, T. D. (2020). Yield benefits of additional pollination to faba bean vary with cultivar, scale, yield parameter and experimental method. *Scientific Reports*, *10*(1), 1–11.

Brittain, C. A., Vighi, M., Bommarco, R., Settele, J., & Potts, S. G. (2010). Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic and Applied Ecology*, *11*(2), 106–115.

Bukovinszky, T., Verheijen, J., Zwerver, S., Klop, E., Biesmeijer, J. C., Wäckers, F. L., Prins, H. H. T., & Kleijn, D. (2017). Exploring the relationships between landscape complexity, wild bee species richness and reproduction, and pollination services along a complexity gradient in the Netherlands. *Biological Conservation*, *214*, 312–319.

Byrne, F., & delBarco-Trillo, J. (2019). The effect of management practices on bumblebee densities in hedgerow and grassland habitats. *Basic and Applied Ecology*, *35*, 28–33.

Carrié, R., Ekroos, J., & Smith, H. G. (2018). Organic farming supports spatiotemporal stability in species richness of bumblebees and butterflies. *Biological Conservation*, *227*, 48–55.

Carvell, C., Jordan, W. C., Bourke, A. F. G., Pickles, R., Redhead, J. W., & Heard, M. S. (2012). Molecular and spatial analyses reveal links between colony-specific foraging distance and landscape-level resource availability in two bumblebee species. *Oikos*, *121*(5), 734–742.

Cole, L. J., Kleijn, D., Dicks, L. V., Stout, J. C., Potts, S. G., Albrecht, M., Balzan, M. V., Bartomeus, I., Bebeli, P. J., Bevk, D., Biesmeijer, J. C., Chlebo, R., Dautartė, A., Emmanouil, N., Hartfield, C., Holland, J. M., Holzschuh, A., Knoben, N. T. J., Kovács-Hostyánszki, A., … Scheper, J. (2020). A critical analysis of the potential for EU common agricultural policy measures to support wild pollinators on farmland. *Journal of Applied Ecology*, *57*(4), 681–694.

Defra. (2007). *Hedgerow survey handbook. A standard procedure for local surveys in the UK*. Department for Environment, Food and Rural Affairs.

Defra. (2020). *Countryside stewardship*. Retrieved from https://www.gov.uk/government/collections/countryside-stewardship-get-paid

Dicks, L. V., Baude, M., Roberts, S. P. M., Phillips, J., Green, M., & Carvell, C. (2015). How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge. *Ecological Entomology*, *40*, 22–35.

Diekötter, T., Kadoya, T., Peter, F., Wolters, V., & Jauker, F. (2010). Oilseed rape crops distort plant–pollinator interactions. *Journal of Applied Ecology*, *47*(1), 209–214.

Evans, L. C., Sibly, R. M., Thorbek, P., Sims, I., Oliver, T. H., & Walters, R. J. (2019). Quantifying the effectiveness of agri-environment schemes for a grassland butterfly using individual-based models. *Ecological Modelling*, *411*, 108798.

Falk, S. J. (2015). *Field guide to the bees of Great Britain and Ireland*. British Wildlife Publishing.

Fijen, T. P. M., Scheper, J. A., Boekelo, B., Raemakers, I., & Kleijn, D. (2019). Effects of landscape complexity on pollinators are moderated by pollinators' association with mass-flowering crops. *Proceedings of the Royal Society B*, *286*(1900), 20190387.

Franzén, M., & Nilsson, S. G. (2010). Both population size and patch quality affect local extinctions and colonizations. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1678), 79–85.

Gardner, E., Breeze, T. D., Clough, Y., Smith, H. G., Baldock, K. C. R., Campbell, A., Garratt, M. P. D., Gillespie, M. A. K., Kunin, W. E., McKerchar, M., Memmott, J., Potts, S. G., Senapathi, D., Stone, G. N., Wäckers, F., Westbury, D. B., Wilby, A., & Oliver, T. H. (2020a). Poll4pop model code from: Reliably predicting pollinator abundance: Challenges of calibrating process- based ecological models. *Zenodo*, https://doi.org/10.5281/zenodo.4001015

Gardner, E., Breeze, T. D., Clough, Y., Smith, H. G., Baldock, K. C. R., Campbell, A., Garratt, M. P. D., Gillespie, M. A. K., Kunin, W. E., McKerchar, M., Memmott, J., Potts, S. G., Senapathi, D., Stone, G. N., Wäckers, F., Westbury, D. B., Wilby, A., & Oliver, T. H. (2020b). Data from: Reliably predicting pollinator abundance: Challenges of calibrating process-based ecological models. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.9cnp5hqfw

Gardner, E., Breeze, T. D., Clough, Y., Smith, H. G., Baldock, K. C. R., Campbell, A., Garratt, M. P. D., Gillespie, M. A. K., Kunin, W. E., McKerchar, M., Memmott, J., Potts, S. G., Senapathi, D., Stone, G. N., Wäckers, F., Westbury, D. B., Wilby, A., & Oliver, T. H. (2020c). Reliably predicting pollinator abundance: Challenges of calibrating process-based ecological models. *Methods in Ecology and Evolution*, *11*(12), 1673–1689.

Garibaldi, L. A., Sáez, A., Aizen, M. A., Fijen, T., & Bartomeus, I. (2020). Crop pollination management needs flower-visitor monitoring and target values. *Journal of Applied Ecology*, *57*(4), 664–670.

Garratt, M. P. D., Breeze, T. D., Jenner, N., Polce, C., Biesmeijer, J. C., & Potts, S. G. (2014). Avoiding a bad apple: Insect pollination enhances fruit quality and economic value. *Agriculture, Ecosystems & Environment*, *184*, 34–40.

Garratt, M. P. D., Coston, D. J., Truslove, C. L., Lappage, M. G., Polce, C., Dean, R., Biesmeijer, J. C., & Potts, S. G. (2014). The identity of crop pollinators helps target conservation for improved ecosystem services. *Biological Conservation*, *169*, 128–135.

Garratt, M. P. D., Senapathi, D., Coston, D. J., Mortimer, S. R., & Potts, S. G. (2017). The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. *Agriculture, Ecosystems & Environment*, *247*, 363–370.

Gathmann, A., & Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, *71*(5), 757–764.

Grab, H., Blitzer, E. J., Danforth, B., Loeb, G., & Poveda, K. (2017). Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. *Scientific Reports*, *7*, 45296.

Grab, H., Poveda, K., Danforth, B., & Loeb, G. (2018). Landscape context shifts the balance of costs and benefits from wildflower borders on multiple ecosystem services. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1884), 20181102.

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589–596.

Hass, A. L., Brachmann, L., Batáry, P., Clough, Y., Behling, H., & Tscharntke, T. (2019). Maize-dominated landscapes reduce bumblebee colony growth through pollen diversity loss. *Journal of Applied Ecology*, *56*(2), 294–304.

Häussler, J., Sahlin, U., Baey, C., Smith, H. G., & Clough, Y. (2017). Pollinator population size and pollination ecosystem service responses to enhancing floral and nesting resources. *Ecology and Evolution*, *7*(6), 1898–1908.

Holland, J. M., Smith, B. M., Storkey, J., Lutman, P. J. W., & Aebischer, N. J. (2015). Managing habitats on English farmland for insect pollinator conservation. *Biological Conservation*, *182*, 215–222.

Holzschuh, A., Dormann, C. F., Tscharntke, T., & Steffan-Dewenter, I. (2013). Mass-flowering crops enhance wild bee abundance. *Oecologia*, *172*(2), 477–484.

Hutchinson, L. A., Oliver, T. H., Breeze, T. D., Bailes, E. J., Brünjes, L., Campbell, A. J., Erhardt, A., Arjen de Groot, G., Földesi, R., García, D., Goulson, D., Hainaut, H., Hambäck, P. A., Holzschuh, A., Jauker, F., Klatt, B. K., Klein, A.-M., Kleijn, D., Kovács-Hostyánszki, A., … Garratt, M. P. D. (2021). Using ecological and field survey data to establish a national list of the wild bee pollinators of crops. *Agriculture, Ecosystems & Environment*, *315*, 107447.

IPBES. (2016). The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. In S. G. Potts, V. L. Imperatriz-Fonseca, & H. T. Ngo (Eds.), *Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, Bonn, Germany (p. 552). https://doi.org/10.5281/zenodo.3402856

Kerr, J. T., Pindar, A., Galpern, P., Packer, L., Potts, S. G., Roberts, S. M., Rasmont, P., Schweiger, O., Colla, S. R., Richardson, L. L., Wagner, D. L., Gall, L. F., Sikes, D. S., & Pantoja, A. (2015). Climate change impacts on bumblebees converge across continents. *Science*, *349*(6244), 177–180.

Kirchweger, S., Clough, Y., Kapfer, M., Steffan-Dewenter, I., & Kantelhardt, J. (2020). Do improved pollination services outweigh farm-economic disadvantages of working in small-structured agricultural landscapes? Development and application of a bio-economic model. *Ecological Economics*, *169*, 106535.

Klein, A.-M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 303–313.

Kremen, C., Williams, N. M., Bugg, R. L., Fay, J. P., & Thorp, R. W. (2004). The area requirements of an ecosystem service: Crop pollination by native bee communities in California. *Ecology Letters*, *7*(11), 1109–1119.

Lindström, S. A. M., Herbertsson, L., Rundlöf, M., Smith, H. G., & Bommarco, R. (2016). Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia*, *180*(3), 759–769.

Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., & Greenleaf, S. (2009). Modelling pollination services across agricultural landscapes. *Annals of Botany*, *103*(9), 1589–1600.

MacInnis, G., Buddle, C. M., & Forrest, J. R. K. (2020). Small wild bee abundance declines with distance into strawberry crops regardless of field margin habitat. *Basic and Applied Ecology*, *44*, 14–23.

Main, A. R., Hladik, M. L., Webb, E. B., Goyne, K. W., & Mengel, D. (2020). Beyond neonicotinoids–wild pollinators are exposed to a range of pesticides while foraging in agroecosystems. *Science of the Total Environment*, *742*, 140436.

Main, A. R., Webb, E. B., Goyne, K. W., & Mengel, D. (2020). Reduced species richness of native bees in field margins associated with neonicotinoid concentrations in non-target soils. *Agriculture, Ecosystems & Environment*, *287*, 106693.

Marja, R., Viik, E., Mänd, M., Phillips, J., Klein, A.-M., & Batáry, P. (2018). Crop rotation and agri-environment schemes determine bumblebee communities via flower resources. *Journal of Applied Ecology*, *55*(4), 1714–1724.

Morandin, L. A., & Kremen, C. (2013). Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications*, *23*(4), 829–839.

Morandin, L. A., Long, R. F., & Kremen, C. (2016). Pest control and pollination cost–benefit analysis of hedgerow restoration in a simplified agricultural landscape. *Journal of Economic Entomology*, *109*(3), 1020–1027.

Nicholson, C. C., Ricketts, T. H., Koh, I., Smith, H. G., Lonsdorf, E. V., & Olsson, O. (2019). Flowering resources distract pollinators from crops: Model predictions from landscape simulations. *Journal of Applied Ecology*, *56*(3), 618–628.

Nowakowski, M., & Pywell, R. F. (2016). *Habitat creation and management for pollinators*. Centre for Ecology & Hydrology.

Olsson, O., Bolin, A., Smith, H. G., & Lonsdorf, E. V. (2015). Modeling pollinating bee visitation rates in heterogeneous landscapes from foraging theory. *Ecological Modelling*, *316*, 133–143.

Perrot, T., Gaba, S., Roncoroni, M., Gautier, J.-L., & Bretagnolle, V. (2018). Bees increase oilseed rape yield under real field conditions. *Agriculture, Ecosystems & Environment*, *266*, 39–48.

Powney, G. D., Carvell, C., Edwards, M., Morris, R. K. A., Roy, H. E., Woodcock, B. A., & Isaac, N. J. B. (2019). Widespread losses of pollinating insects in Britain. *Nature Communications*, *10*(1), 1018.

Pywell, R. F., Heard, M. S., Woodcock, B. A., Hinsley, S., Ridding, L., Nowakowski, M., & Bullock, J. M. (2015). Wildlife-friendly farming increases crop yield: Evidence for ecological intensification. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1816), 20151740.

R Core Team. (2018). *Language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Redhead, J. W., Dreier, S., Bourke, A. F. G., Heard, M. S., Jordan, W. C., Sumner, S., Wang, J., & Carvell, C. (2016). Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. *Ecological Applications*, *26*(3), 726–739.

Redhead, J. W., Oliver, T. H., Woodcock, B. A., & Pywell, R. F. (2020). The influence of landscape composition and configuration on crop yield resilience. *Journal of Applied Ecology*, *57*(11), 2180–2190.

Redhead, J. W., Woodcock, B. A., Pocock, M. J. O., Pywell, R. F., Vanbergen, A. J., & Oliver, T. H. (2018). Potential landscape-scale pollinator networks across Great Britain: Structure, stability and influence of agricultural land cover. *Ecology Letters*, *21*(12), 1821–1832.

Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I., & Holzschuh, A. (2015). Annual dynamics of wild bee densities: Attractiveness and productivity effects of oilseed rape. *Ecology*, *96*(5), 1351–1360.

Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., & Holzschuh, A. (2014). Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape Ecology*, *29*(3), 425–435.

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S. G., Rundlöf, M., Smith, H. G., & Kleijn, D. (2013). Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – A meta-analysis. *Ecology Letters*, *16*(7), 912–920.

Scholefield, P. A., Morton, R. D., Rowland, C. S., Henrys, P. A., Howard, D. C., & Norton, L. R. (2016). Woody linear features framework, Great Britain v. 1.0. NERC Environmental Information Data Centre (Dataset). https://doi.org/10.5285/d7da6cb9-104b-4dbc-b709-c1f7ba94fb16

Schürch, R., Accleton, C., & Field, J. (2016). Consequences of a warming climate for social organization in sweat bees. *Behavioral Ecology and Sociobiology*, *70*(8), 1131–1139.

Senapathi, D., Carvalheiro, L. G., Biesmeijer, J. C., Dodson, C.-A., Evans, R. L., McKerchar, M., Morton, R. D., Moss, E. D., Roberts, S. P. M., Kunin, W. E., & Potts, S. G. (2015). The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1806), 20150294.

Shaw, R. F., Phillips, B. B., Doyle, T., Pell, J. K., Redhead, J. W., Savage, J., Woodcock, B. A., Bullock, J. M., & Osborne, J. L. (2020). Mass-flowering crops have a greater impact than semi-natural habitat on crop pollinators and pollen deposition. *Landscape Ecology*, *35*(2), 513–527.

Sheffield, C. S., Westby, S. M., Smith, R. F., & Kevan, P. G. (2008). Potential of bigleaf lupine for building and sustaining *Osmia lignaria* populations for pollination of apple. *The Canadian Entomologist*, *140*(5), 589–599.

Staley, J. T., Sparks, T. H., Croxton, P. J., Baldock, K. C. R., Heard, M. S., Hulmes, S., Hulmes, L., Peyton, J., Amy, S. R., & Pywell, R. F. (2012). Long-term effects of hedgerow management policies on resource provision for wildlife. *Biological Conservation*, *145*(1), 24–29.

Stuligross, C., & Williams, N. M. (2020). Pesticide and resource stressors additively impair wild bee reproduction. *Proceedings of the Royal Society B*, *287*(1935), 20201390.

Sullivan, M. J. P., Pearce-Higgins, J. W., Newson, S. E., Scholefield, P., Brereton, T., & Oliver, T. H. (2017). A national-scale model of linear features improves predictions of farmland biodiversity. *Journal of Applied Ecology*, *54*(6), 1776–1784.

Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, *56*(7), 1585–1596.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters*, *8*(8), 857–874.

Ullmann, K. S., Meisner, M. H., & Williams, N. M. (2016). Impact of tillage on the crop pollinating, ground-nesting bee, *Peponapis pruinosa* in California. *Agriculture*, *Ecosystems & Environment*, *232*, 240–246.

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, *6*(11), 961–965.

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, *46*(1), 187–193.

Wood, T. J., Holland, J. M., & Goulson, D. (2015). Pollinator-friendly management does not increase the diversity of farmland bees and wasps. *Biological Conservation*, *187*, 120–126.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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