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

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11 **Running headline:** Boundary features can stabilise bee populations

Abstract

1. Pollinators experience large spatio-temporal 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 1m grassy margins, hedgerows and wide 4m agri-environment margins) to support and stabilise pollinator populations and pollination service in agricultural landscapes under crop rotation. Assuming a six-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.

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, but the more stable delivery compensated for this by nonetheless increasing the minimum pollination service delivered in any given year.

5. *Synthesis and applications.* 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— pollinators, pollination service, agroecology, stability, variability, resilience, crop rotation, hedgerows, field margins

1 Introduction

Pollination is a key ecosystem service to global agriculture, enhancing production in ~75% of global crop species (Klein et al., 2007; Potts 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 (Potts 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

48 have been linked with disruptions to plant-pollinator networks (Redhead et al., 2018) and crop pollination deficits
49 have already been recorded (Garratt et al., 2014a).

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

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

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

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

83 While several studies have demonstrated the benefits of boundary features for pollinator abundance and
84 diversity (e.g. Scheper et al., 2013; Albrecht et al., 2020), less is known about their influence on temporal
85 stability of pollinator abundance and pollination services, partly because field monitoring over long timescales

86 is challenging. Since consistency of yield is crucial to farmers, increasing attention is being paid to the role of
87 landscape structure in functional stability and crop yield resilience (e.g. Redhead et al., 2020). Floral margins
88 can serve as refuges for pollinators in years of successive cereal crops (Marja et al. (2018)) and help sustain
89 pollinators after local crop bloom (Sheffield et al. (2008)). Thus, boundary features could stabilise pollinator
90 populations when resources vary temporally across multiple timescales. This includes resource timescales shorter
91 than the lifetime of individual pollinators (e.g. weekly, where mass-flowering occurs briefly each year in the same
92 location) and multi-year timescales longer than the lifetime of individual pollinators (e.g. where resource-rich
93 mass-flowering crops only occur in a given field once in a set number of years). The latter is relevant to the
94 large-scale spatio-temporal dynamics of crop-rotated landscapes

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

110 2 Materials and Methods

111 2.1 Model description

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

120 The model accounts for seasonal differences in the floral cover offered by each habitat and outputs visitation
121 rate per pixel per season, based on the amount of time bees from all nests spend foraging in each pixel. Solitary

122 bees are assumed to be active only during one (user-selected) season, reflecting the short flight periods of the
123 majority of solitary species (Falk, 2015). Social bees (e.g. bumblebees) are assumed to be active across three
124 seasons. The model simulates their colony-building behaviour by assuming queens forage during season 1 to
125 produce workers, which forage during season 2 to produce additional workers. The total resources gathered by
126 all workers during season 3 then determines the number of new queens produced by the nest at the end of the
127 active period. In contrast, the number of new females produced by a solitary bee nest is solely dependent on the
128 resources gathered by the original nest-founding female. The model can be run for multiple years by using the
129 dispersed reproductives from the previous year as the starting population for the next and as such can reproduce
130 source/sink population dynamics.

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

133 2.2 Model parameterisation

134 We run the model for ground-nesting bumblebees (e.g. *Bombus terrestris* etc.) and ground-nesting solitary bees
135 (e.g. *Andrenidae*). These are the two largest wild bee guilds in the UK (Falk, 2015) and include many of the key
136 pollinators of OSR and field beans (Hutchinson et al., 2021). We take model parameters for these guilds from
137 G2020. These consist of estimates of nest density and foraging/dispersal distances derived from the literature
138 (Greenleaf et al., 2007; Gathmann and Tschardt, 2002; Franzén and Nilsson, 2010 as used in Dicks et al., 2015;
139 Häussler et al., 2017), plus estimates of floral cover, foraging attractiveness and nesting attractiveness derived from
140 an expert opinion questionnaire, where experts scored habitats based on their experience (maximum $n = 10$ UK
141 pollinator experts; see G2020 for details). We adopt the expert opinion estimates from the G2020 study, rather
142 than the calibrated values, due to the ecological unfeasibility of some of the calibrated values. G2020 showed
143 this model parameterisation incorporating expert opinion estimates produces model predictions that significantly
144 agree with the observed abundances from transect surveys at 239 sites distributed across Great Britain.

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

157 For solitary bees, we retained the original spring and summer seasonal definitions used in G2020 (i.e. not
158 subdividing spring into early and late), since solitary bees do not produce workers, typically have shorter flight

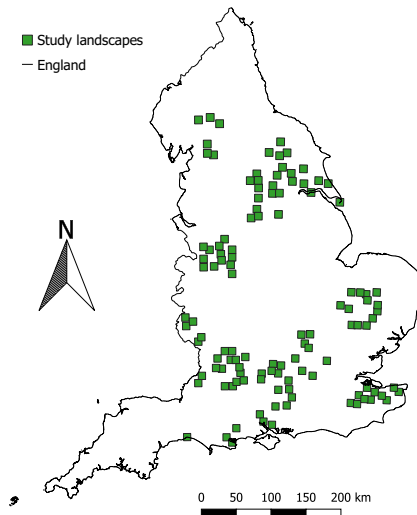


Figure 1: Locations of study landscapes within England, UK.

159 periods and different species show different emergence times. We run the model twice for solitary bees: once
 160 to simulate spring-flying solitary species and once to simulate summer-flying solitary species, where these are
 161 assumed independent of the number of spring-flying solitaires, i.e. representing different species with later flight
 162 periods.

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

166 2.3 Study landscapes

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

177 2.3.1 Boundary feature maps

178 Each landscape is accompanied by three boundary feature maps. The first of these represents hedgerow locations
 179 ('hedges') derived from the CEH Woody Linear Features Database (Scholefield et al., 2016), which has been

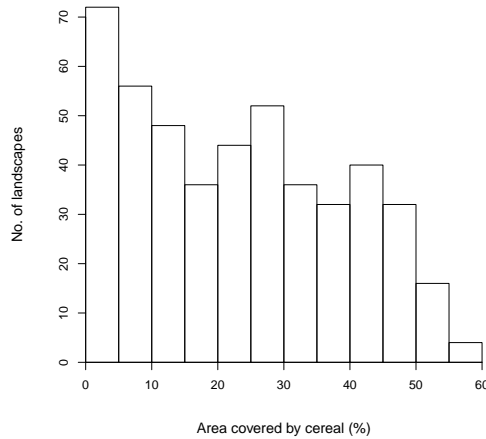


Figure 2: Variation in cereal crop area across the 117 $10 \times 10 \text{ km}^2$ study landscapes.

180 shown to predict abundance of insect species in agricultural landscapes (Sullivan et al., 2017). Since the database
 181 does not capture 100% of hedgerows, this is augmented by adding hedgerows around the perimeter of any land
 182 parcel claiming for agri-environment hedgerow options through the Countryside Stewardship Scheme in 2016. We
 183 assume all hedgerows are 2m wide (width corresponding to ‘favourable condition’; Defra, 2007).

184 The second boundary feature map represents agri-environment margins (‘agri-env.’) and incorporates all grassy
 185 buffer strips, fallow margins, flower-rich margins and ditches whose presence or management was subsidised during
 186 2016 by the Countryside Stewardship Scheme (see G2020 for a detailed list of the relevant scheme options). A 4m
 187 width is assumed for all these features (since 4–6m is recommended for buffer strips; e.g. Defra, 2020) and, due to
 188 lack of information on the features’ exact locations, the features were mapped around the entire perimeter of the
 189 land parcel associated with the claim. This approximation allows us to identify fields in the landscape with more
 190 generous margins, as well as those with fallow areas or enhanced floral resources. The agri-environment margin
 191 map is therefore the combination of these wide grassy, fallow and flower-rich margins around specific fields.

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

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

198 2.4 Crop rotation sequence

199 The landcover maps described in §2.3 represent a snapshot of the study landscapes in the year 2016. We impose a
 200 six-year crop rotation sequence of cereal-cereal-OSR-cereal-cereal-field bean and generate crop rotated landscapes
 201 for the five subsequent years of this rotation. We note that many of the study landscapes likely undergo a much
 202 longer rotation in reality (e.g. with many more consecutive years of cereal), while organic and low input systems
 203 often have more variable/diverse rotations. However, we choose a six-year rotation to facilitate simulation within

204 a reasonable computation time and because shorter rotations are recommended to more sustainably manage soil
205 health/fertility.

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

213 2.5 Boundary feature simulations

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

217 We test five scenarios:

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

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

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

233 2.6 Data analysis

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

$$rms_{i,j,k} = \sqrt{\sum_{t=2}^{t=20} (v_{i,j,k}(t) - mean_{i,j,k})^2} \quad (1)$$

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

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

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

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

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

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

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

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

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

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

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

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

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

252 The magnitude and significance of the fitted coefficient β therefore allows us to compare how the fractional
 253 change in time-averaged mean visitation rate (or rms variability in visitation rate) relative to the no-boundary-

254 features value depends on the area within the landscape covered by that boundary feature.

255 3 Results

256 3.1 Ground-nesting bumblebees

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

266 The wide range in $\Delta_{mean,i,k}$ and $\Delta_{rms,i,k}$ values shown in Fig. 3 reflects the fact that both boundary-feature
267 area and rotating-crop area varied across the landscapes. Fitting equations 8 and 9 allowed us to separate
268 these effects and isolate the relative effect per unit area of each type of boundary feature. This demonstrated that
269 landscapes with a greater area of boundary features showed higher time-averaged mean landscape-level bumblebee
270 visitation rates (i.e. larger bumblebee populations) relative to the no-boundary-features scenario (Fig. 4, left-hand
271 plots, green bars). This was true for all seasons. The agri-environment margins produced the greatest fractional
272 change in mean visitation rate per unit area, likely due to these features providing a combination of nesting and
273 floral resources often clustered together in nearby fields collectively managed by a single participating farm. In
274 the all-boundary-features scenario, the fractional change in mean visitation rate per unit area was intermediate
275 between the standard narrow margins and hedge only scenarios, despite including all boundary features. This is
276 due to these more common boundary features covering a far greater area within the study landscapes than the
277 agri-environment margins (Fig. S1) and so dominating the overall landscape response.

278 The seasonal landscape-level bumblebee visitation rates were also more stable relative to the no-boundary-
279 features scenario in landscapes with a greater area of boundary features (Fig. 4, right-hand plots, green bars). In
280 early spring, hedgerows provided the strongest stabilising effect, i.e. most negative $\Delta_{rms,i,k}$ coefficient, indicating
281 a $\sim 7\%$ reduction in rms variability per unit increase in hedgerow area. In late spring, during mass crop flowering,
282 agri-environment margins provided no statistically significant stabilising effect on bumblebee landscape-level vis-
283 itation (likely due to their small total area within each study landscape with respect to the flowering crops) but
284 they did provide the largest (and a statistically significant) stabilising effect in summer ($\sim 12\%$ rms variability
285 reduction per unit area).

286 The in-crop bumblebee visitation rate showed similar trends to the landscape-level visitation (Fig. 4; blue
287 and orange bars). Landscapes with a greater area of boundary features showed significantly higher time-averaged
288 field bean and OSR visitation rates ($> 10\%$ higher per unit area of hedges or agri-environment margins during
289 peak late-spring flowering) and significantly more stable field bean and OSR visitation rates ($\sim 8\%$ more stable

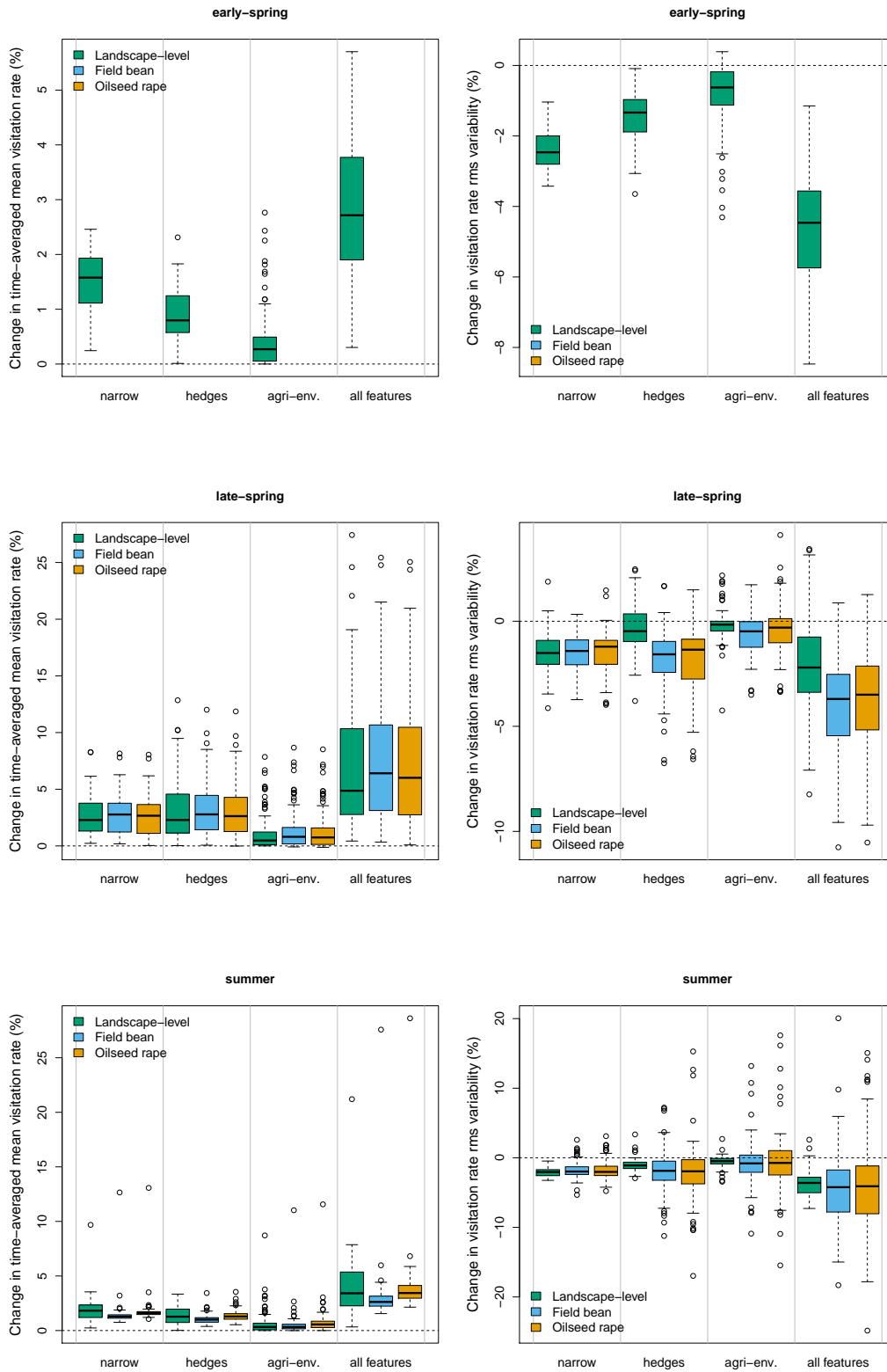


Figure 3: Change in ground-nesting bumblebee landscape-level, field bean and OSR visitation rates for each boundary feature scenario, relative to the no-boundary-features scenario, for the 117 study landscapes. Left-hand panels show percentage change in the mean visitation rate across the 20 year simulation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

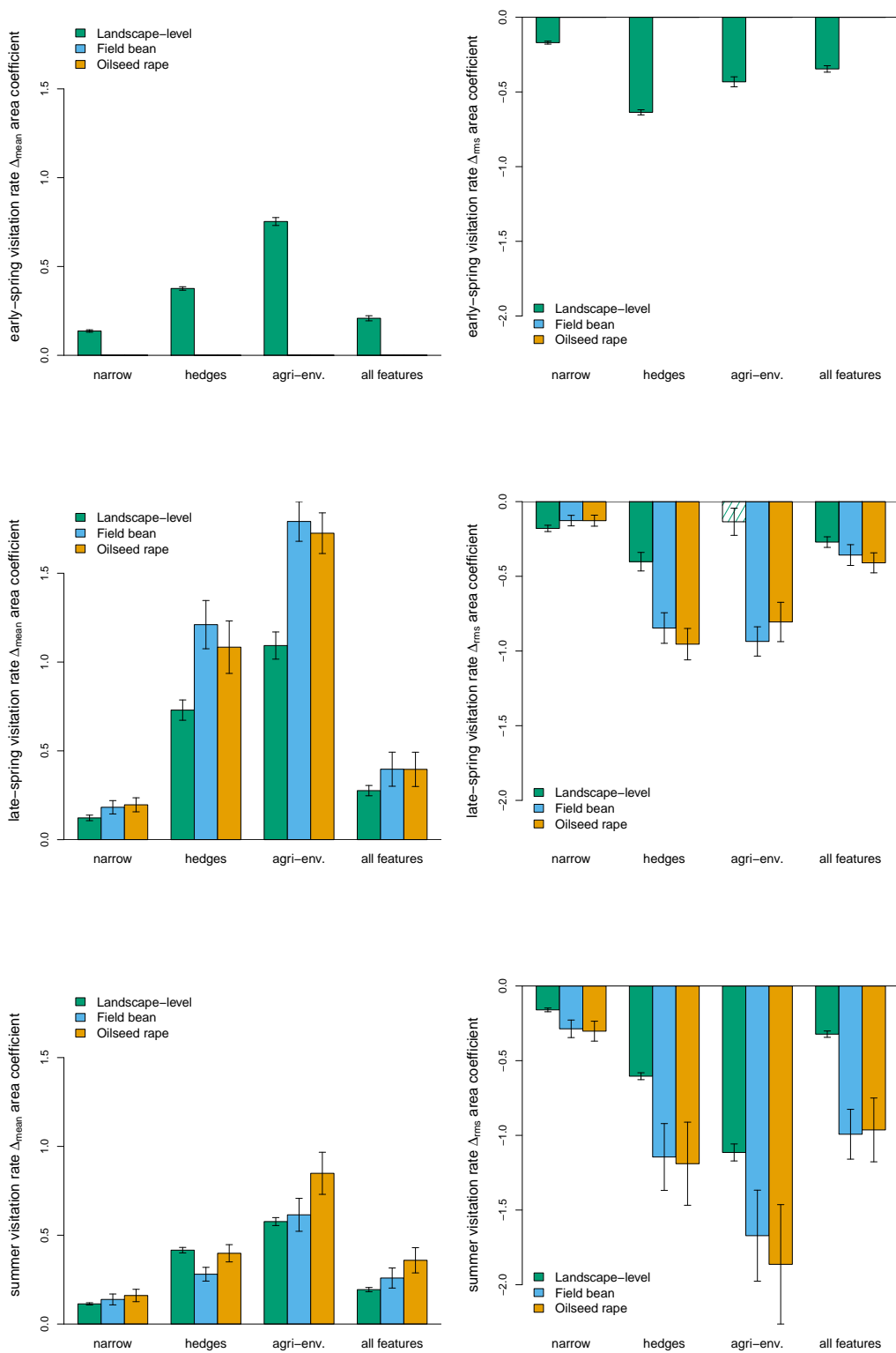


Figure 4: Dependence of fractional change in ground-nesting bumblebee visitation rate on boundary-feature area, where the fractional change is calculated relative to the no-boundary-features scenario and bar heights represent area coefficients for landscape-level (green), field bean (blue) and OSR (orange) 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.

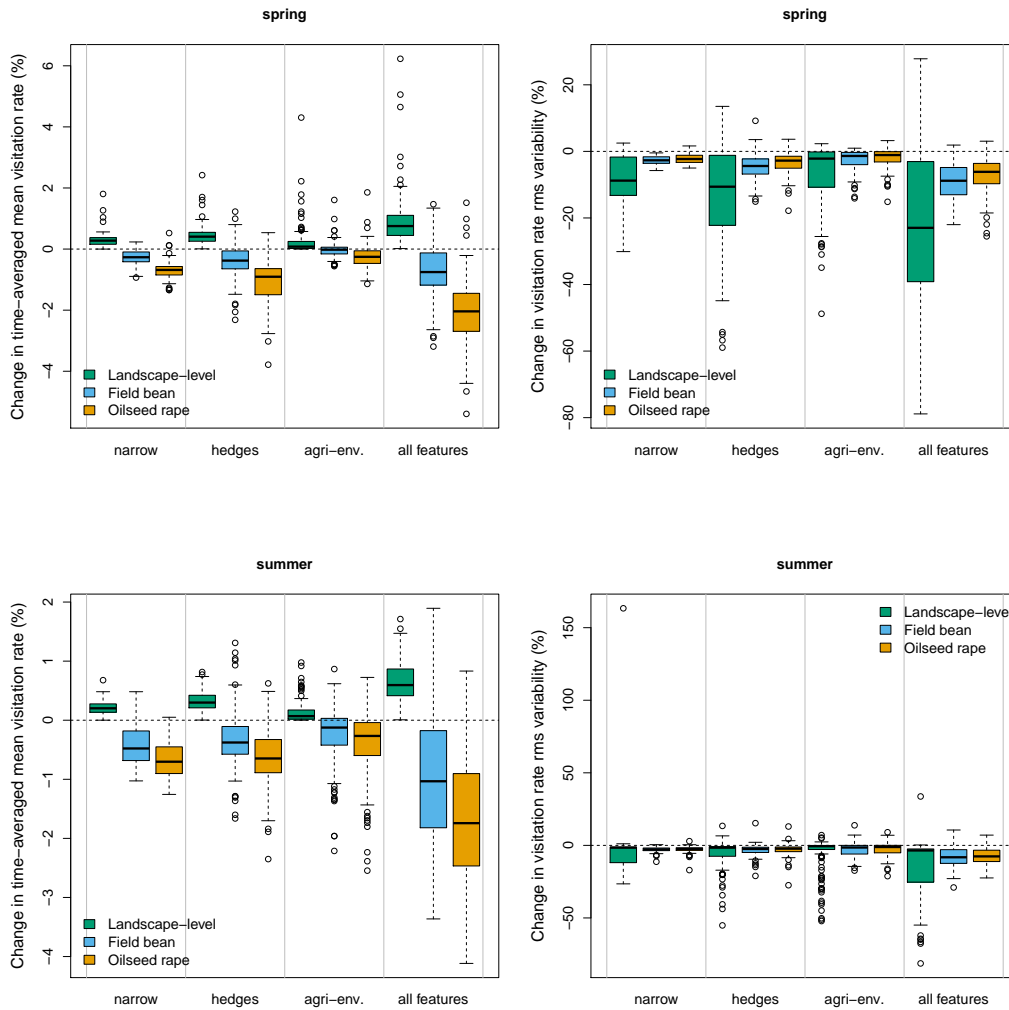


Figure 5: Change in ground-nesting solitary bee landscape-level, field bean and OSR visitation rates for each boundary feature scenario, relative to the no-boundary-features scenario, for the 117 study landscapes. Left-hand panels show percentage change in the mean visitation rate across the 20 year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

290 per unit area for the same boundary features and season) with respect to the no-boundary-features scenario.
 291 In many cases, the effect per unit area of boundary feature was stronger for in-crop bumblebee visitation rates
 292 than at landscape-level, due to the in-crop visitation including less dilution from stable sub-populations based in
 293 non-crop landcovers remote from agricultural boundary features.

294 3.2 Ground-nesting solitary bees

295 For solitary bees, when boundary features were included in the simulations, the landscapes typically showed higher
 296 landscape-level visitation rates that were more stable over time. Although the increase in mean landscape-level
 297 visitation was generally small ($< 1\%$), the reduction in landscape-level variability when all boundary features
 298 were included was as large 80% in some landscapes, with median reductions of $\sim 20\%$ and $\sim 5\%$ during spring and
 299 summer, respectively (Fig. 5, green boxes). The in-crop field bean and OSR solitary bee visitation rates were also

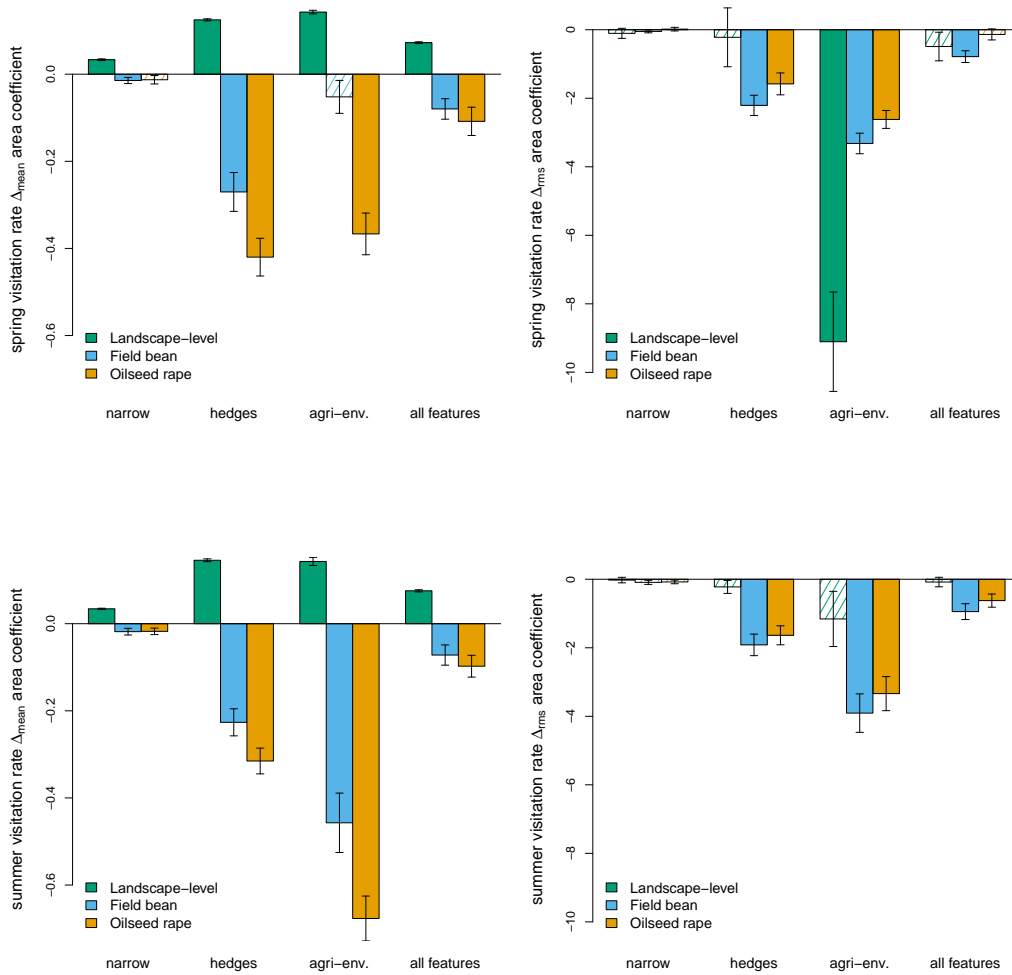


Figure 6: Dependence of fractional change in ground-nesting solitary bee visitation rate on boundary-feature area, where the fractional change is calculated relative to the no-boundary-features scenario and bar heights represent area coefficients for landscape-level (green), field bean (blue) and OSR (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.

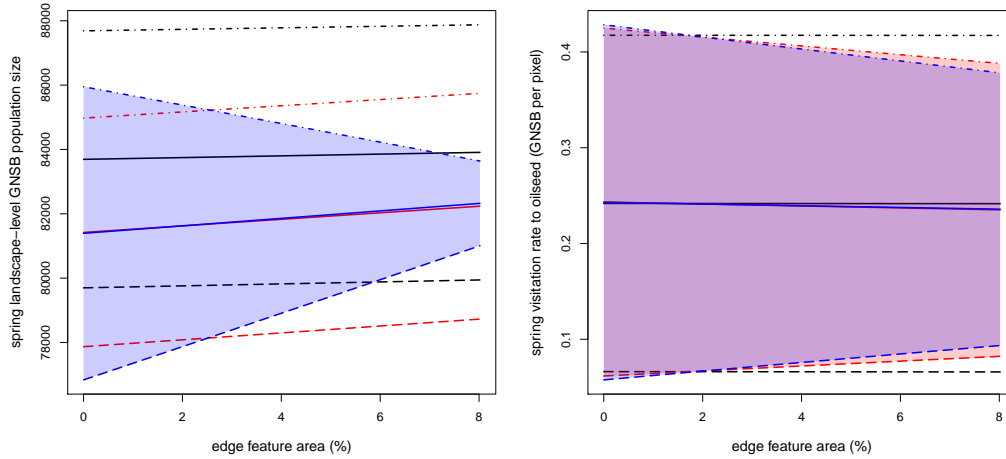


Figure 7: Predicted ground-nesting solitary bee landscape-level population (left) and OSR visitation rate (right) trends with increasing boundary-feature area for a highly arable study landscapes (cereal fraction = 54.4%). Trends are calculated using Equations 8 and 9, the fitted coefficients from Fig. 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, 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.

300 typically more stable over time (median values of $\sim 5\text{-}10\%$ across all landscapes for the ‘all features’ scenario), but
 301 the time-averaged mean visitation rates to these crops were generally lower, with median values indicating 1–2%
 302 reductions for the ‘all features’ scenario (Fig. 5, blue and orange boxes).

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

316 The fits also confirmed that landscapes with a greater area of boundary features are predicted by the model
 317 to show a lower time-averaged mean solitary bee visitation rate to field bean and OSR compared to the no-
 318 boundary-features scenario (Fig. 6; blue and orange bars). Although the standard narrow margins scenario

319 does not show any significant decrease in $\Delta_{rms,i,k}$ with increasing area, the other boundary feature scenarios
320 do (with the exception of the spring all-boundary-features scenario), confirming an increase in boundary-feature
321 area significantly decreases solitary bee in-crop visitation rate rms variability in these cases (Fig. 6, right-hand
322 plots, blue and orange bars). Fig. 7 (right-hand panel) illustrates how this decrease in variability amplitude
323 can compensate for the small reduction in time-averaged mean visitation rate, such that the expected minimum
324 yearly crop visitation rate (mean-rms) is nonetheless higher in the scenario with boundary features present than
325 without.

326 4 Discussion

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

334 4.1 Impacts of boundary features on bee population stability

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

347 For ground-nesting solitary bees, the simulations show that boundary features likewise increase populations,
348 but only wide agri-environment interventions provide any significant stabilising effect and only during spring.
349 This is due to their shorter lifetimes, lack of colony building behaviour, and shorter foraging/dispersal distances.
350 In most species, a solitary bee female provisions her own nest and the offspring emerge the following year.
351 Other more complex/bivoltine life histories exist for some species (e.g. *Andrena trimmerana* – Falk, 2015), but
352 these are not simulated by the model, which assumes independent spring-flying and summer-flying solitary bee
353 populations. Consequently, the simulated solitary bee populations increase with the nesting opportunities the

354 boundary features offer, but their productivity is still strongly influenced by immediate floral resources during their
355 short foraging window, which includes the variable resources from nearby rotated crops. As such, for solitary
356 bees, boundary features do not generate the more extensive stabilising influence experienced by the longer-
357 lifetime bumblebees. Furthermore, the shorter foraging/dispersal distances of solitary bees ($\sim 100 - 200\text{m}$ versus
358 $500 - 1000\text{m}$ for bumblebees; Gathmann and Tschardt, 2002; Carvell et al., 2012) increase their reliance upon
359 permanently concurrent patches of good floral and nesting resources and they cannot take advantage of boundary
360 features to effectively shift their population centre in pursuit of the rotating mass-flowering crops like the more
361 mobile bumblebees. Thus, while boundary features can boost the solitary bee population, larger permanent semi-
362 natural habitat patches within agricultural settings will be more effective for maintaining landscape-level solitary
363 bee population stability, providing these patches contain good nesting resources and sufficient phenologically
364 concurrent floral resources to self-sustain the solitary bee population within the habitat patch, without resorting
365 to resources beyond it.

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

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

381 Boundary features can provide additional benefits to bumblebee and solitary bee population size and stability
382 beyond those captured by our simulations. Firstly, primitively eusocial/bivoltine solitary bee species, which were
383 not modelled, may benefit from the longer-term resource availability provided by boundary features in a similar
384 manner to bumblebees, potentially experiencing a greater stabilising effect than demonstrated by our simulations
385 for single-brood solitary bees. Secondly, we have used general floral attractiveness scores for bumblebees and
386 solitary bees that assume both guilds are able to make some use of mass-flowering crop resources. Species within
387 these guilds not physically able to access these resources (e.g. due to flower morphology) will potentially experience
388 even greater benefits from increasing alternative habitat via boundary features. Thirdly, although sophisticated
389 and capable of reproducing observed bee abundances (Gardner et al., 2020b), our model does not include the
390 movement of males or the explicit movement paths and mortality of dispersing females beyond their inability
391 to find a suitable nest site. Instead, a standard dispersal distance is assumed independent of landscape context.

392 This may be a reasonable assumption for strongly philopatric solitary bees, but may not be for bumblebees with
393 longer dispersal distances (Redhead et al., 2016). If males and dispersing queens are less likely to successfully
394 cross open post-harvest fields, semi-natural boundary features may provide bumblebees with crucial pathways
395 for genetic exchange, as well as resources to sustain dispersing females. Understanding these core aspects of
396 species' ecology and incorporating explicit sub-models of this movement process (e.g. similar to those developed
397 for butterflies; Evans et al., 2019) would allow improved estimates of the importance of boundary features for
398 different bee species.

399 **4.2 Impacts of boundary features upon the stability of crop pollination ser-** 400 **vices**

401 Examining the predicted visitation rates to field bean and OSR showed that the larger, more stable bumblebee
402 populations produced by increasing boundary features translated directly into significantly larger and more stable
403 pollination service from bumblebees to these mass-flowering crops. In the model, the early-spring-foraging queens
404 gather more resources when boundary features are present, producing larger numbers of workers to forage on the
405 late-spring flowering crops. The trends imply that if standard 1m grassy field margins were replaced by wider
406 4m agri-environment margins with their enhanced floral and nesting resources, then the stabilising effect on crop
407 visitation from bumblebees would be up to ten times stronger per unit area of boundary feature. However, these
408 effects may take some years to become fully established in reality (Morandin et al., 2016) and would depend on
409 the quality of the boundary feature (e.g. Garratt et al., 2017).

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

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

426 Again, we note boundary features are likely to produce additional crop pollination service benefits beyond
427 those captured by our simulations. Primitively eusocial/bivoltine solitary bee species, which were not modelled,
428 may show increases in crop visitation more similar to bumblebees than the single-brood solitary bees. Our

429 guild-level model also does not capture the fact that boundary features can promote a more diverse solitary bee
430 community (Sheffield et al., 2008). This benefits crop pollination service because the short flight periods of many
431 solitary bee species, and the influence of weather on both bee and plant phenology, can easily cause mismatches
432 between crop flowering and solitary bee emergence. A more diverse solitary bee community with a variety of
433 emergence times increases the likelihood that crop flowering occurs within the flight period of at least one solitary
434 species each year, regardless of when the crop flowers.

435 **4.3 Management implications**

436 **4.3.1 Yield stabilisation**

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

445 **4.3.2 Timing of crop sowing/flowering**

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

455 **4.3.3 Crop rotation sequence**

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

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

470 **4.3.4 Lockstepping**

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

478 **4.3.5 Boundary feature management**

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

499 The projected benefits of boundary features could be further enhanced by tailoring their floral composition,

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

506 **4.3.6 Accounting for other sources of variability**

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

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

517 **5 Conclusions and Recommendations**

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

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

- 529 **1. Combinations of boundary features.** Maximum benefit is likely to be achieved by combining multiple
530 boundary features (hedgerows, grassy margins and flower-rich margins), since different boundary features
531 provide benefits in different seasons. Ensure chosen boundary feature combinations provide good quality
532 nesting resources within foraging range ($< 500\text{m}$) of a succession of complimentary and abundant floral
533 resources of diverse floral morphologies (see e.g. Nowakowski and Pywell, 2016).
- 534 **2. Larger permanent patches of semi-natural habitat, e.g. permanent wide (4m) margins, are**

535 **necessary for stabilising less mobile solitary bee populations.** Solitary bees have faster life histo-
536 ries, shorter foraging range and often have strong philopatry (particularly in species with specialised soil
537 requirements for nesting), so narrow margin approaches are not as effective for stabilising their populations
538 under crop rotation as they are for stabilising the more mobile bumblebees. Therefore, dedicate larger
539 permanent semi-natural habitat patches to maintaining strong solitary bee populations and let the crops
540 come to them.

541 **3. Synchronise boundary feature management with crop rotation and rotate mass-flowering**
542 **crops sequentially through adjacent fields, where possible.** This will maintain resources for infield
543 bee populations when mass-flowering crops are absent and will better enable populations of more mobile
544 species to follow mass-flowering crops, especially if guided by provision of overwintering sites and early
545 floral resources.

546 **4. Increase boundary feature area and reduce distance between boundary features (i.e. reduce**
547 **field sizes), where possible.** The stabilising benefit of boundary features on bee populations will be
548 optimised where boundary features are spaced within the typical dispersal distance (200m–1800m, depend-
549 ing on species). The stabilising benefit of boundary features on pollination service will be optimised where
550 boundary features providing nesting and sustained floral resources occur within the typical foraging range
551 (100–500m) of pollinator-dependent crops.

552 **6 Author Contributions**

553 EG devised and carried out the research. EG wrote the manuscript with contributions from TB. YC provided
554 poll4pop pollinator model. All other authors provided comments on the manuscript and/or datasets for model
555 validation.

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559 ESRC and the Scottish Government.

560 **8 Data Availability**

561 Validation dataset deposited in the Dryad repository: <https://doi.org/10.5061/dryad.9cnp5hqfw>. Process-based
562 pollinator model freely available to download from <https://github.com/yclough/poll4pop> (doi:10.5281/zenodo.4001015).

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