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

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34 Abstract

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

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

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

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

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

62 1 Introduction

63 Animal pollinators support reproduction in an estimated 87.5% of flowering plant species
64 worldwide, including over three quarters of the world's leading food crops (Klein et al.,
65 2007, Ollerton et al., 2011). In England, the most important pollinator-dependent crops are
66 oilseed rape (*Brassica napus*; hereafter OSR), field beans (*Vicia faba*), orchard fruit
67 (apples, pears, and plums) and soft fruit (mainly strawberries and raspberries) (Breeze et
68 al., 2020; DEFRA, 2017). Pollination of these crops is mainly carried out by wild,
69 unmanaged pollinators – principally bumblebees and solitary bees (Blitzer et al., 2016;
70 Garratt et al., 2014a; Hutchinson et al., 2021; Klatt et al., 2013). There is evidence of
71 widespread declines in wild bee populations in Great Britain between 1980 and 2013
72 (Powney et al., 2019), echoing a global trend of decline (IPBES, 2016). This can impact
73 food security where floral visitation is insufficient to achieve optimal yield in pollinator-
74 dependent crops (Garratt et al., 2014a; Holland et al., 2020). Even where this risk is not

75 imminent, declining wild bee abundance and diversity can leave areas vulnerable to future
76 shocks in bee populations or instability of other ecosystem services (Hutchinson et al.,
77 2021; Senapathi et al., 2015).

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

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

95 Many options serve a broad environmental purpose aligned to the farming system such as
96 hedgerow management, grass margins and low-input grassland. Others are specifically
97 designed to restore or maintain habitats such as semi-natural grassland, moorland, and
98 woodland, while capital items provide funding for one-off activities such as hedge planting.
99 Where these options and items increase the quality and quantity of nesting and/or floral

100 resources in a landscape, they can be valuable to pollinators depending on species'
101 preferences (Vaudo et al., 2015). Some CS options have been explicitly designed to
102 provide floral resources for wild bees and other pollinators in arable farms, (e.g. AB1 –
103 Nectar flower mix, and AB16 – Autumn sown bumblebird mix) and its 'Wild Pollinator and
104 Farm Wildlife Package' encourages farmers to bundle these with options that may provide
105 nesting resources (e.g. hedgerows and field corner management).

106 Several studies demonstrate that these AES features can boost wild bee species richness
107 and abundance at field and farm scale (Balfour et al., 2015; Heard et al., 2012; Scheper et
108 al., 2015). The relationship between AES and crop pollination services is more complex
109 and less well understood. A relationship between provision of AES features in agricultural
110 landscapes and crop pollination services has been demonstrated empirically at farm and
111 field scale (Blaauw and Isaacs, 2014; Morandin et al., 2016; Nicholson et al., 2017; Pywell
112 et al., 2015), but, due to different bees foraging ranges and preferences (Kennedy et al.,
113 2013) this is not consistent across feature type (Albrecht et al., 2020).

114 However, AES feature effectiveness at local scale does not necessarily translate into
115 whole-scheme effectiveness at national scale. Schemes are not mandatory and even
116 where farmers do participate, the choice of options implemented may not necessarily be
117 the most effective at supporting wild bees due implementation cost influencing option
118 choice (Austin et al., 2015). Since empirical approaches are unfeasible at national scale,
119 detailed modelling that incorporates how bees move around the landscape to nest, forage
120 and reproduce is needed to estimate the impact of AES on pollination service. The
121 process-based pollinator model developed by Lonsdorf et al. (2009) and later
122 developments of it (Häussler et al., 2017; Olsson et al., 2015) have this capability and have
123 already been applied at regional scale to examine the impact of interventions (Cong et al.,
124 2014; Davis et al., 2017; Häussler et al., 2017), while the latest state-of-the-art version

125 ('poll4pop') has recently been validated in Great Britain for four wild bee guilds (Gardner et
126 al., 2020).

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

138 2 Methodology

139 All modelling/data processing was carried out in ArcGIS 10.7 (ESRI, 2019) and Python 2.7 /
140 3.5. The Poll4pop model source code was transcribed from R (R Core Team, 2018) to
141 Python to facilitate integration with ArcGIS and improve processing times.

142 2.1 Model Description

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

149 The model requires a land cover raster detailing the land class assigned to each cell as
150 well as a rasterised map showing the area of 'edge' land classes (features smaller than the
151 cell resolution – 25m² in our case) within each cell. Each land class has a score
152 representing the amount of floral resource provided during a given season (floral cover),
153 the attractiveness of that floral resource to the guild (floral attractiveness; representing its
154 nutritional quality), and its attractiveness as a nesting resource to that guild (nesting
155 attractiveness). Floral cover and floral attractiveness are multiplied to generate a floral
156 resource raster by season. The edge features are incorporated by taking the area-weighted
157 sum of the edge and non-edge features in a given cell.

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

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

174 guild. In the final active season for social guilds the resources are used to produce new
175 reproductive females.

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

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

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

191 We note that these predicted visitation rates do not include visitation by other non-modelled
192 pollinators, that crop yield ultimately depends non-linearly on this visitation rate and that the
193 relationship between our predicted visitation rates and the rate required for optimum
194 pollination of any given crop is still uncertain (see Discussion). Nonetheless, by simulating
195 foraging and population processes, the model represents the best tool currently available

196 for assessing how fine-scale changes in habitat provision/configuration may influence bee
197 abundance and visitation rates at landscape-scale.

198

199 2.2 Model Parameterisation and Validation

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

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

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

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

- 220 • Orchards: the G2020 floral cover parameter was allocated 90% to early spring and
221 10% floral to late spring.
- 222 • All other land classes: the G2020 floral cover parameter was allocated 50% to early
223 spring and 50% to late spring.

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

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

230 2.3 AES Present and AES Absent Scenarios

231 In order to make predictions for pollinator abundances and visitation rates with, and in the
232 absence of, current AES management, we generated land cover and edge input rasters at
233 25m² resolution for two scenarios: '*AES_Present*' representing the scenario where the AES
234 management was present, and '*AES_Absent*' representing the scenario where AES
235 management was absent. The year 2016 was chosen because it was the most recent to
236 have agricultural, non-agricultural and AES spatial data at sufficient resolution. A brief
237 overview of the process is given in the following section, with a detailed description
238 provided in the Supplementary Material.

239 2.3.1 Source landcover data

240 Land cover and edge feature information were sourced to represent as closely as possible
241 the coverage of non-agricultural land, crops and permanent grassland, and land under agri-
242 environment scheme (AES) option management for England during the year 2016. We

243 included a 5km buffer zone into Scotland and Wales to eliminate edge effects based on the
244 largest mean dispersal distance parameter (1km for bumblebee nesting).

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

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

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

267 ES and CS datasets only provide a LPIS reference and the length or area of feature. So,
268 we implemented a process to split up LPIS parcel polygons into smaller components
269 representing the individual AES features and the remainder of the parcel (See
270 Supplementary Material Section 2.3). Where the AES option type was too small to be
271 resolved at 25m² cell resolution in the subsequent raster conversion, we used an
272 analogous process to create polylines (e.g. at the polygon boundary) appropriate to the
273 option.

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

282 2.3.2 Parameterising changes in land cover habitat quality

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

289 Land in AES was assigned an *AES_Present* land class and an *AES_Absent* land class with
290 reference to Defra Reports BD2302 (University of Hertfordshire, 2009) as refined in
291 BD5007 (University of Hertfordshire, 2011); – hereafter, BD2302/5007). These reports

292 describe the expected land cover resulting from the option (used to generate *AES_Present*)
293 and the absence of management (used to generated *AES_Absent*). Assignment of
294 *AES_Present* and *AES_Absent* land classes to CS options was made using an
295 'Equivalency Table' provided by Natural England (the scheme developer) that links these
296 options to their ES equivalents (Natural England, 2018 *pers. comm*). Option descriptions
297 provided in scheme manuals (Natural England, 2013; 2015) were used where required.

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

315 Land not in AES was assigned the same land cover class as G2020 with the exception of
316 semi-natural grassland categories in LCM (acid grassland, neutral grassland, calcareous

317 grassland) which were assigned to a semi-improved grassland category rather than an
318 unimproved grassland category as per the LCM metadata (CEH, 2017). As this land was
319 outside AES in both scenarios, the classification was the same in *AES_Present* and
320 *AES_Absent*. The final parameter values used for all land classes, the weighting rules for
321 new land classes, and the guild-specific parameters are shown in the Supplementary
322 Material (Table S1).

323 2.3.3 Assessment of change in abundance and visitation rates

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

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

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

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

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

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

365 *Table 1: Land Categories*

| Land Category | Description |
|----------------------|--------------------|
|----------------------|--------------------|

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

366

367 2.4 Exemplar Area

368 To illustrate the fine-scale effects predicted by our 25m² resolution simulations at farm-
369 scale, we selected an exemplar area in western England to present alongside the national
370 maps. This area was chosen because it is one of the few areas in England to grow all four
371 pollinator-dependent crops and it represents a heterogeneous landscape incorporating a
372 variety of agri-environment interventions.

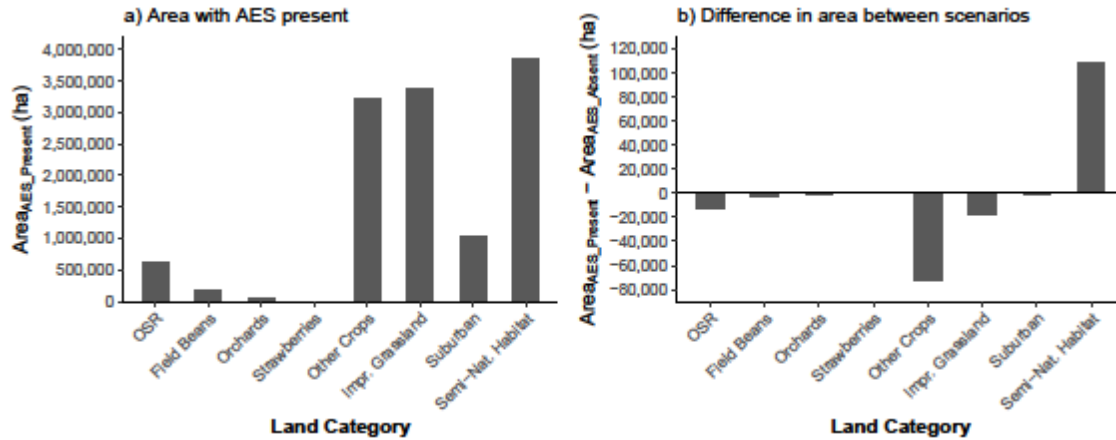
373

374 3 Results

375 3.1 Area and distribution of crops and land under AES

376 The pollinator-dependent crops OSR (621,014 ha) and field beans (189,332 ha) were
377 grown across much of lowland England during 2016, while orchard fruit (39,335 ha) and
378 strawberries (2,914 ha) were concentrated in certain areas of south-east and western
379 England (Figure 1a; Figure S13a-b; Figure S14a-b). Otherwise, England's agricultural area
380 was dominated by other crops (not pollinator-dependent) and improved grassland. There
381 was over 3.5M ha of semi-natural habitat of potential value to wild bees including
382 hedgerows, ditches, grass/flower margins, heathland, and woodland. ~1.5M ha of this was
383 under AES management (Figure S15a) but the rest was outside the CS and ES schemes
384 (Figure S15b). Suburban parks and gardens (highly valuable pollinator habitat) covered
385 ~1.0M ha.

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



396

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

400 **3.2 Impact of AES participation on pollinator abundance at national level**

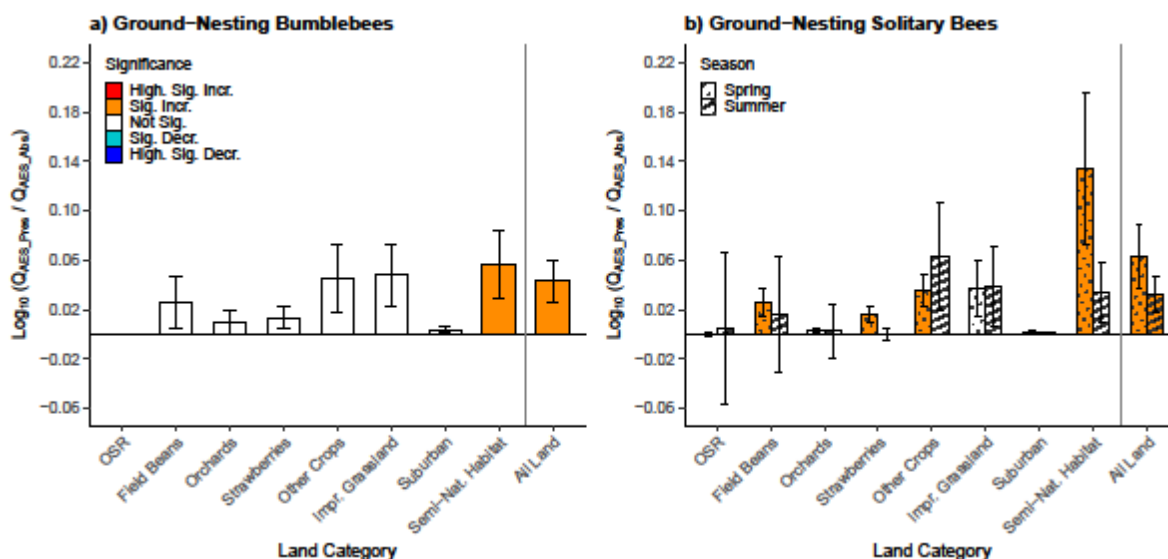
401 Nest productivity (number of new reproductive females produced per cell) is predicted to be
 402 significantly higher for ground-nesting guilds when AES management is present (Figure 2 –
 403 ‘All land’) with relative increases of 10.4% for ground-nesting bumblebees and 15.4% /
 404 7.8% for spring-active / summer-active ground-nesting solitary bees.

405 Nest density is also predicted to be significantly higher for ground-nesting guilds when AES
 406 management is present (Figure 3, ‘All land’) with increases of 4.6% for ground-nesting
 407 bumblebees and 16.2% for spring-active ground-nesting solitary bees. The predicted
 408 increase in nest density for summer-active ground-nesting solitary bees is not significant.

409 Semi-natural habitat shows the largest and consistently significant nest density increases
 410 (6.6% and 36.9% for the above-mentioned guilds respectively) across the land categories
 411 and this drives the change in the ‘All land’ category. Significant nest density increases in
 412 crop and improved grassland categories for ground-nesting solitary bees are relatively
 413 small (2.8% – 9.0%) while no significant overall increase is predicted for tree-nesting
 414 bumblebees or cavity-nesting solitary bees (Figures S4, S5 in Supplementary Material).

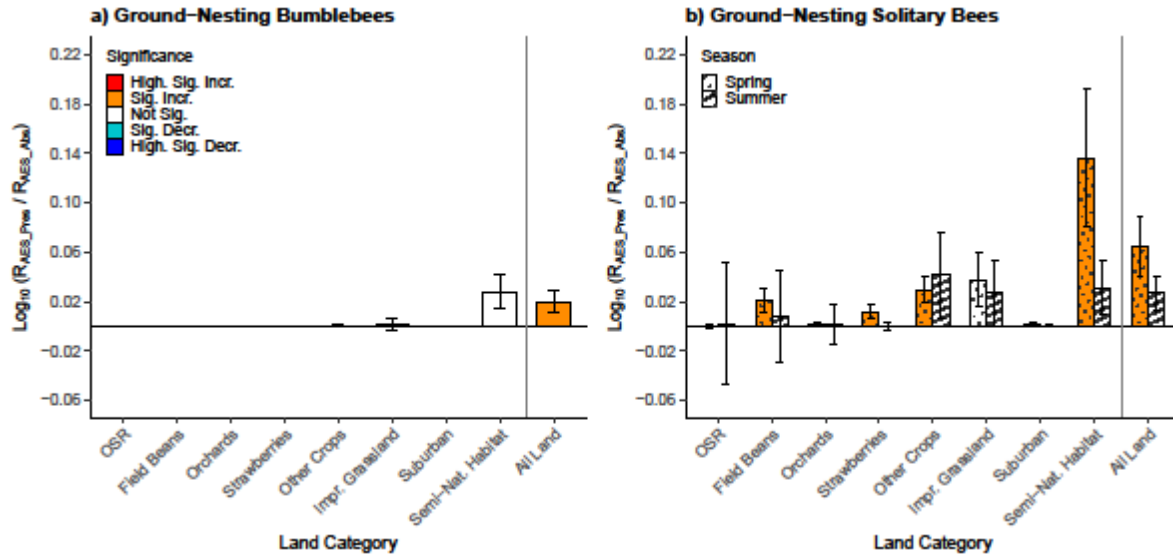
415

416 AES management is also predicted to have a significant overall positive impact on ground-
 417 nesting bumblebee worker production in late spring (increase of 8.15%; Figure 4b ‘All
 418 Land’) although semi-natural habitat is the only land category to show a significant increase
 419 (11.5% equivalent). Overall increases in worker production are predicted for early spring
 420 but these are not significant given current uncertainties, the exception being a small but
 421 significant predicted increase in the worker population for nests in orchards during early
 422 spring (2.5% equivalent). No significant overall change in tree-nesting bumblebee worker
 423 production is predicted, though the results do show a similar significant increase for
 424 orchards in early spring (Figure S3 in Supplementary Material.).



425

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



432

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

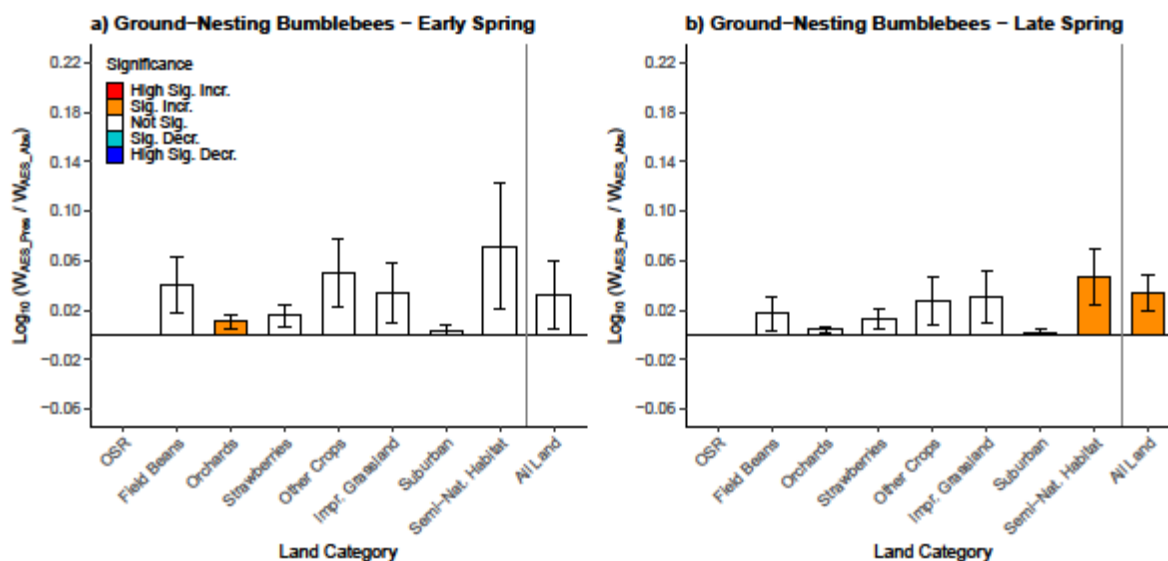
439 3.3 Impact of AES participation on floral visitation rate at national level

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

447 Although the model predicts increased visitation rate to OSR and field beans during peak
 448 flowering (Late Spring) due to AES management, this increase is only significant for the
 449 case of ground-nesting solitary bees to field beans where visitation rises by 6.2% (Figure
 450 5). An increase of similar scale and significance to field beans is also predicted for cavity-
 451 nesting solitary bees. The absolute change in both cases is not large and is from a low

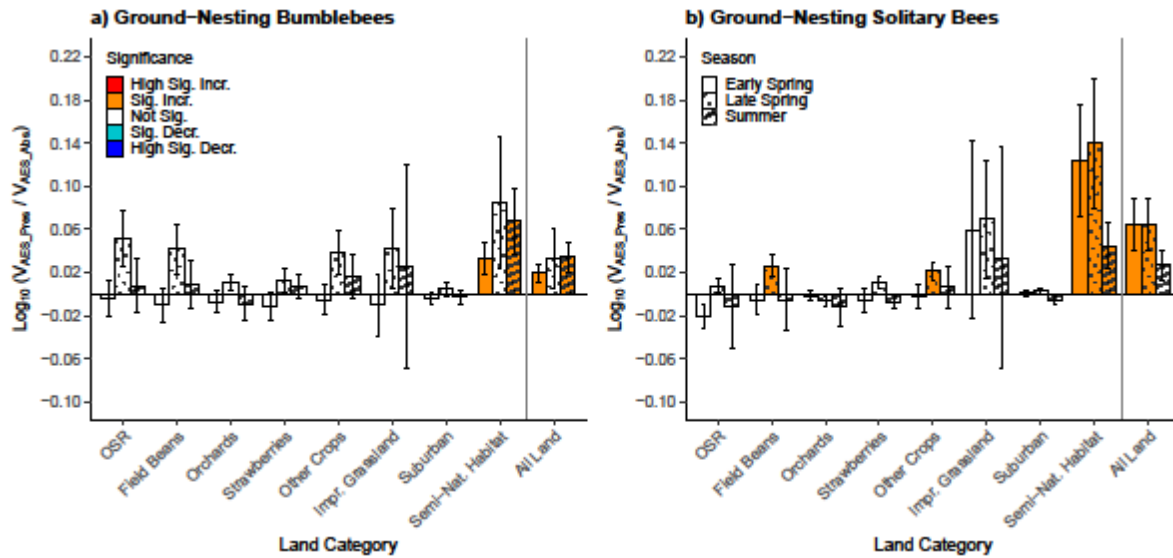
452 base (e.g. V_s in *AES_Absent* for field beans is 0.19 for ground-nesting solitary bees
 453 compared to 7.9 for ground-nesting bumblebees; Figure S9 in the Supplementary Material).

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



461

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



468

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

476

477 3.4 Impact of AES participation on floral visitation rate at cell-level

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

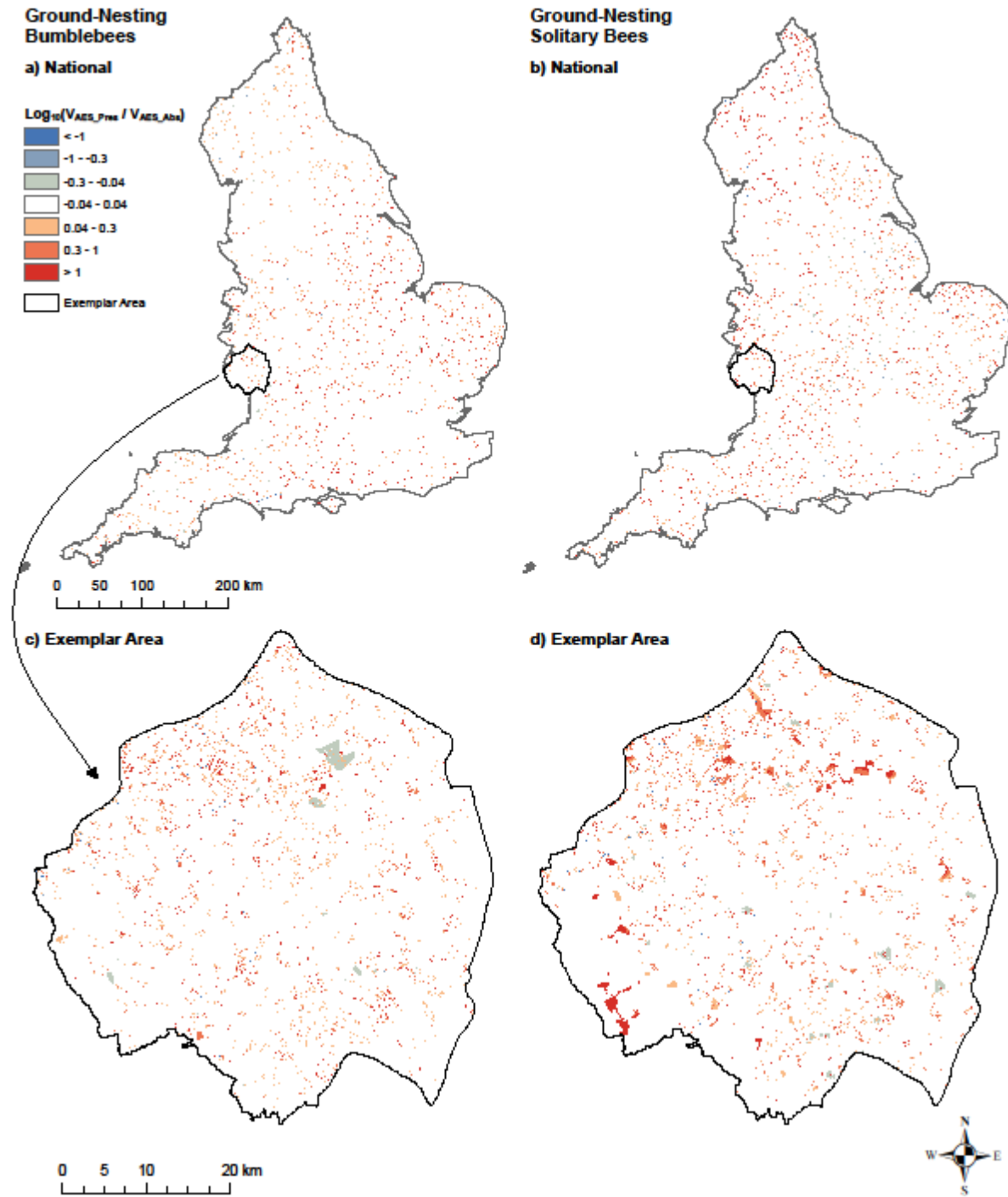
488 the AES cells. The effect is less evident in other seasons (see Figure 6 for early spring and
489 Figure S16 in the Supplementary Material for summer).

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

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

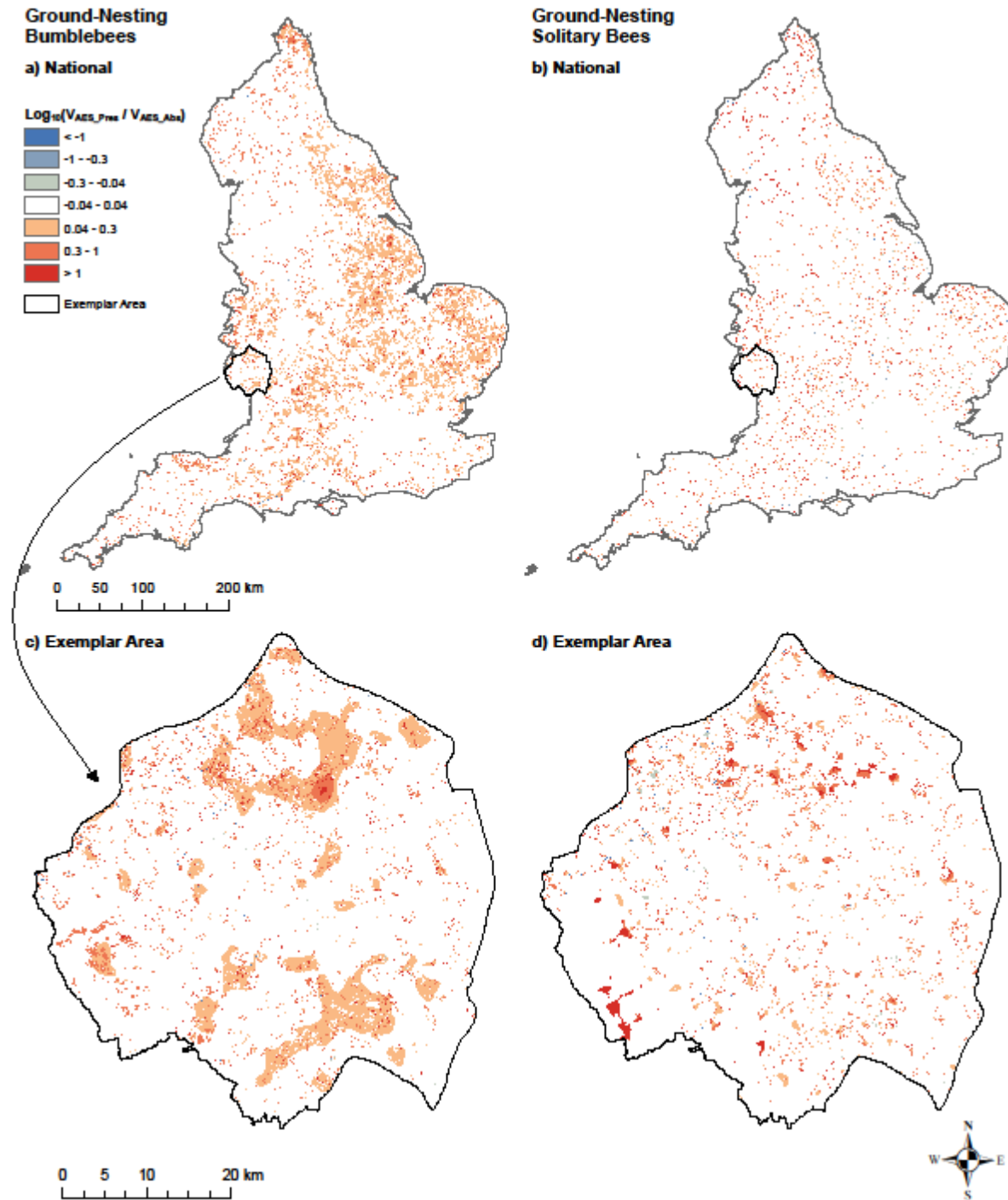
505 Likewise, very few cells are predicted to receive significantly more bee visitation in Summer
506 (Figure S16, Supplementary Material).

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



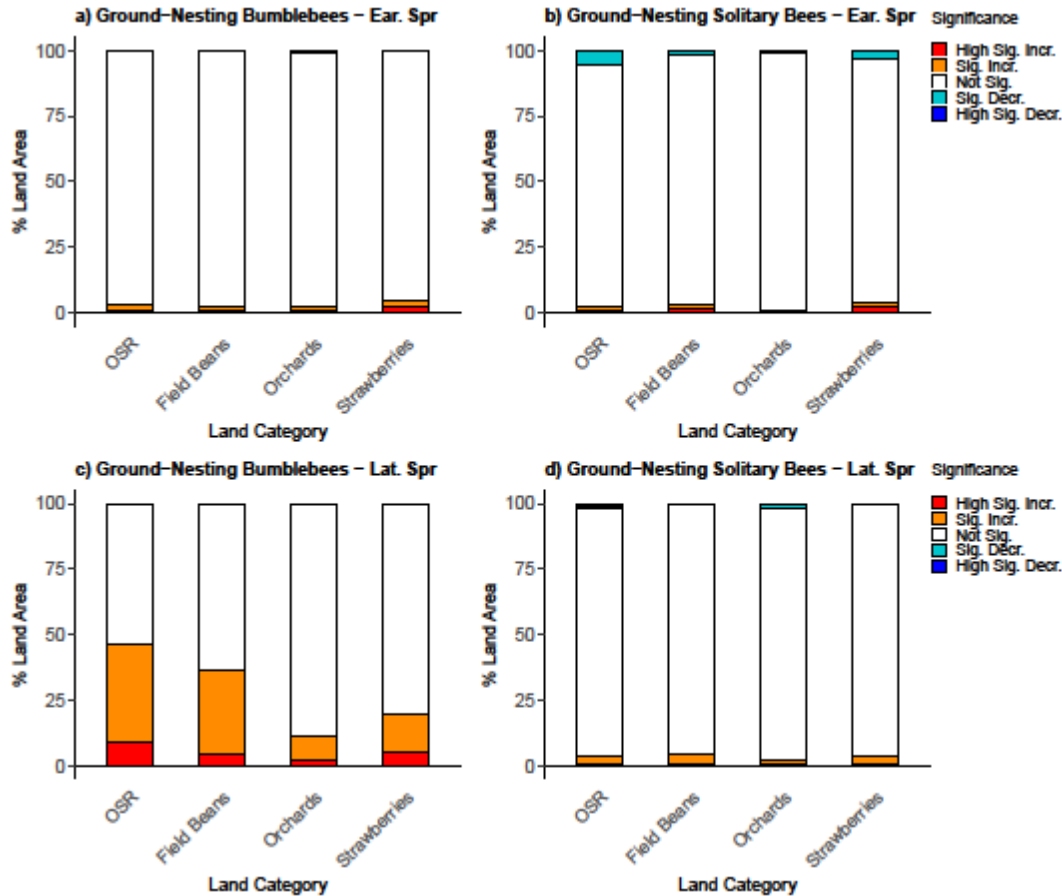
512

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



518

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



524

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

531 4 Discussion

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

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

547 4.1 Impact of AES on pollinator abundance

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

561 Interestingly, our modelling suggests that the significant increases in nest productivity for
562 ground-nesting bumblebees, induced by AES participation, are not matched by significant

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

569 Predicted increases in abundance (number of new reproductive females) are predominantly
570 associated with semi-natural habitats, which are typically of higher floral and nesting quality
571 under AES participation. We do also predict an increase in solitary bee nest abundance in
572 some crop fields (Figure 2b, Figure S2b), although abundance in these areas still remains
573 low compared to semi-natural habitats (Figure S6b, d). The experts who provided the
574 model's habitat scores assigned some limited solitary bee nesting value to certain crop
575 types (Tables S9, S10), assumed to represent nesting opportunities in bare but untilled
576 margins/tramlines, etc. The predicted increase in in-crop nests therefore likely reflects the
577 fact that solitary bee reproductive females produced within adjacent AES features face
578 limited availability of their preferred nesting habitat, due to their limited dispersal range (β_n
579 = 100m vs 1000m for bumblebees) and the relatively low semi-natural habitat coverage in
580 arable areas (Figure S15).

581 4.2 Impact of AES on pollination services

582 The simulations predict significant and often large (2 to 10-fold) increases in visitation at
583 cells under AES management (where floral and nesting values have generally increased
584 relative to their value in *AES_Absent*). There is also a significant but generally smaller
585 “neighbourhood effect” representing 0.1 to 2-fold changes in predicted visitation to
586 surrounding cells outside AES management, where resource value is otherwise
587 unchanged. The magnitude and direction of this neighbourhood effect depends on the guild

588 and season. Where foraging is done by reproductive females (i.e. solitary bees in all
589 seasons and bumblebees in early spring), increased neighbourhood visitation only occurs if
590 the nesting density has increased sufficiently to offset the relative increase in floral value
591 within the AES cell (Zamorano et al., 2020). Otherwise, there will be no change or even
592 potentially sink effects where foragers are drawn away from neighbouring cells (see Figure
593 S17 for tree-nesting bumblebees in early spring). For bumblebees in later seasons,
594 workers do the foraging so floral resource increases support higher worker production rates
595 and thus higher neighbourhood foraging rates without the need for increases in nest
596 density (Riedinger et al., 2014).

597 The neighbourhood effect extends over a larger area for ground-nesting bumblebees
598 compared to ground-nesting solitary bees due to their larger foraging and dispersal ranges
599 ($\beta_f = 530\text{m}$ vs 191m ; $\beta_n = 1000\text{m}$ vs 100m). This enables bumblebee populations to forage
600 and disperse more widely, especially in more fragmented landscapes (Cranmer et al.,
601 2012), so extending their neighbourhood effect. To encourage more solitary bee visitation
602 into crops, schemes would need to provide larger, contiguous habitat features that better
603 account for their limited dispersal range (Martínez-Núñez et al., 2020; Woodcock et al.,
604 2013). In so doing, schemes would also help increase the diversity of pollinators provided
605 thus increasing the resilience of the service.

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

612 4.2.1 Effect on OSR and field beans

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

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

635 4.2.2 Effect on orchard fruit and strawberries

636 At national scale, there was no significant increase in visitation to orchard or strawberry
637 cells due to AES during their peak flowering seasons (early spring and summer,

638 respectively). Both crops are predominantly located in areas of England that have relatively
639 low AES participation (Figure S14, S15). Field studies elsewhere in Europe have found
640 significantly lower populations of wild bees in the vicinity of commercial orchards (Eeraerts
641 et al., 2017; Marini et al., 2012). This was attributed to lack of habitat diversity, suggesting
642 that greater targeting of AES towards orchards would be beneficial for visitation, especially
643 in more intensive agricultural landscapes (Holzschuh et al., 2012). Landscape
644 fragmentation and simplification around strawberry crops is also associated with lower wild
645 bee abundance and lower crop visitation rates (Bukovinszky et al. 2017; Castle et al., 2019;
646 Connelly et al., 2015).

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

654 Early spring orchard visitation is dependent on reproductive females, and we do not predict
655 nest density increases in orchards (Figure 3). Although workers are available to forage on
656 strawberry crops, their peak flowering season (summer) coincides with that of many AES
657 interventions, potentially causing competition for pollinators. Significant increases in
658 visitation to both these crops will therefore only be achieved if AES provide a large increase
659 in nest density (which increases the absolute number of foragers) relative to the increase in
660 floral value provided (which decreases the relative attractiveness of the crop). Scheme
661 design may also need to change to increase the financial incentive available to fruit

662 growers as current AES payment rates may not cover the income foregone in more
663 productive agricultural areas where these crops are grown (Lastra-Bravo et al., 2015).

664

665 4.3 Caveats

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

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

684 Our study has sought to predict the extent to which participation in AES at scheme level,
685 given current uptake patterns, has changed wild bee guild abundances and flower visitation

686 rates. The geographic variation in magnitude and significance of the effect will depend on
687 the type, quantity, quality (relative resource value-add) and placement of the AES resource
688 with respect to crops or other areas of interest. The relative importance of these factors and
689 the relative importance of individual interventions in driving these predicted scheme-level
690 changes will be investigated in forthcoming work.

691 5 Conclusions and Recommendations for Policy

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

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

- 705 • **Floral resource provision.** Our predictions for ground-nesting bee populations
706 align with monitoring data suggesting a slowing of the decline in recent years for
707 generalist bee species due to AES (Powney et al., 2019) and with estimates that a
708 2% land allocation to floral cover options within AES would provide sufficient

709 resource for common wild bee species (Dicks et al., 2015). Schemes should
710 therefore continue to incentivise floral resource provision.

711 • **Nesting resource provision.** We identified nest site limitation as preventing
712 populations from fully benefiting from the increased floral resource provided by AES
713 features and as a contributing factor in our prediction for lack of significant national
714 increase in crop visitation. Schemes should enhance the uptake and sophistication
715 of options that provide nesting resources, especially in orchard- and strawberry-
716 growing regions. Interspersing larger, more contiguous patches of semi-natural
717 habitat within arable areas may also better support short-range solitary bee
718 populations and their pollination services.

719 • **Resource diversity.** Tree-nesting and cavity nesting bee species have habitat
720 requirements that are not well-catered for in current AES. To increase populations
721 of these guilds, schemes should increase the range of interventions that provide
722 specialist nesting and floral resources. Although more bespoke and locally specific
723 features may be required to support some species, AES could support these guilds
724 generically through options that create/manage hedgerows, trees, and scrub (in
725 potentially good alignment with current carbon sequestration goals that also favour
726 such options; Summers et al. (2021)).

727

728 6 Author contributions

729 MI conceived the ideas, carried out the research and wrote the manuscript. TB and EG
730 contributed to conceptual development and manuscript revisions. YC and EG provided the

731 poll4pop model and parameters which MI adapted and applied to this context. All other
732 authors provided comments on the manuscript and/or datasets for model validation.

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739

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