



HAL
open science

Landscape floral resources provided by rapeseed correlate with next-year reproduction of cavity-nesting pollinators in a national participatory monitoring program

Victor van Der Meersch, Olivier Billaud, Magali San Cristobal, Aude Vialatte, Emmanuelle Porcher

► To cite this version:

Victor van Der Meersch, Olivier Billaud, Magali San Cristobal, Aude Vialatte, Emmanuelle Porcher. Landscape floral resources provided by rapeseed correlate with next-year reproduction of cavity-nesting pollinators in a national participatory monitoring program. *Landscape Ecology*, 2022, 10.1007/s10980-021-01353-0 . hal-03407457

HAL Id: hal-03407457

<https://hal.science/hal-03407457>

Submitted on 28 Oct 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Landscape floral resources provided by rapeseed correlate**
2 **with next-year reproduction of cavity-nesting pollinators**
3 **in a national participatory monitoring program**

4 **Victor Van der Meersch · Olivier**
5 **Billaud · Magali San Cristobal · Aude**
6 **Vialatte · Emmanuelle Porcher ·**

7
8 Received: date / Accepted: date

9 **Abstract Context** Wild pollinators depend on floral resources available
10 in the landscape, partly provided by mass flowering crops (MFCs), such as
11 rapeseed or sunflower. MFCs are however often grown conventionally, implying
12 insecticide use, with potential negative effects on pollinators.

13 **Objectives** To understand whether and to what extent these crops could
14 contribute to the maintenance of pollinator populations, we investigated the

Grants or other notes about the article that should go on the front page should be placed here. General acknowledgments should be placed at the end of the article.

Victor Van der Meersch
Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France

Olivier Billaud
Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France

Magali San Cristobal
Dynamique et Ecologie des Paysages Agriforestiers (DYNAFOR), Institut national de recherche pour l'agriculture, l'alimentation et l'environnement, Université de Toulouse, Castanet Tolosan, France

Aude Vialatte
Dynamique et Ecologie des Paysages Agriforestiers (DYNAFOR), Institut national de recherche pour l'agriculture, l'alimentation et l'environnement, Université de Toulouse, Castanet Tolosan, France

Emmanuelle Porcher
Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France
E-mail: emmanuelle.porcher@mnhnfr

15 inter-annual correlation between MFC resources and the reproduction of cavity-
16 nesting pollinators (solitary bees and wasps) at a national scale.

17 **Methods** We studied a standardized citizen science dataset, in which farm-
18 ers collected data on the abundance of sealed tubes in trap nests, between
19 2012 and 2017, in nearly 600 fields distributed across France. We modelled the
20 relation between nesting and landscape resources of the current and previous
21 year, taking local farming practices into account.

22 **Results** Pollinator nesting was positively correlated with the quantity of
23 rapeseed floral resources the year preceding observations, as well as with the
24 area of permanent meadows. On the contrary, we found more variable relations
25 with sunflower floral resources, depending on the type of sealing material,
26 hence likely on the phenology of pollinators. Our models also confirm that
27 local practices should be accounted for when assessing the influence of the
28 landscape context, although their effects were difficult to interpret.

29 **Conclusions** That solitary bee and wasp reproduction is likely to be posi-
30 tively and durably affected by rapeseed cover. Moderate areas of rapeseed
31 may help maintaining pollinators, in combination with semi-natural habitats,
32 which provide more diverse and stable food and nesting sites.

33
34 **Keywords** agriculture; · biodiversity; · citizen science; · Osmia; · solitary
35 bees; · pollination; · floral resources; · mass-flowering crops

Submitted Version

1 Introduction

Agriculture and biodiversity are inter-linked. The observed trend toward the intensification of farming practices and the homogenization of landscapes over the past decades have triggered significant negative impacts on insect diversity and abundance (Benton et al. 2002; Sánchez-Bayo and Wyckhuys 2019). In particular, pollinators are known to decline because of several human-related drivers, including habitat loss and use of agrochemicals (Potts et al. 2010; Vanbergen and the Insect Pollinators Initiative 2013). This major loss of insects could have negative effects on ecosystem functioning, as insects play a central role in a variety of processes, including pollination: 80% of wild plants are estimated to depend on animals for pollination (Ollerton, Winfree, and Tarrant 2011), and 35% of global agricultural production comes from crops that depend on pollinators (Klein et al. 2007). In turn, many pollinator species depend at least partially on floral resource availability and accessibility (Potts et al. 2003). The spatial and temporal distribution of floral resources is therefore essential for pollinators, especially for central place foragers such as wild bees, which are not spared from human disturbance (Biesmeijer et al. 2006; Goulson, Lye, and Darvill 2008; Potts et al. 2010; Burkle, Marlin, and Knight 2013; Woodcock et al. 2016) and cannot follow the seasonality of flowering from one area to another. They may be more efficient pollinators of wild plants and crops than honeybees (Garibaldi et al. 2014; Mallinger and Gratton 2015), and thus important for supporting pollinator-dependent crops and sustaining pollination services in agricultural areas.

In agricultural landscapes, floral resources for pollinators are provided both by wild plants and by mass flowering crops (MFCs): the former provide less abundant but more constant resources than crops, while the latter provide massive amounts of resources but during a restricted period of flowering. Although wild bees seem to depend more on wild floral resources than on MFCs (Rollin et al. 2013), many of them, including solitary bees, are still known to use MFCs (Jauker, Bondarenko, et al. 2012; Le Féon et al. 2013). Besides, the balance between positive and negative effects of MFCs on wild bees remains unclear. On the one hand, MFCs provide both pollen and nectar resources that positively affect solitary bee species richness (Diekötter et al. 2014), abundance (Le Féon et al. 2013; Riedinger et al. 2015) and reproduction (Holzschuh et al. 2012; Jauker, Peter, et al. 2012), even though some studies found a negative effect (Holzschuh et al. 2016; Shaw et al. 2020). On the other hand, MFCs are often associated with intensive agriculture, which comes with a simplification of landscapes, including fewer semi-natural landscape elements providing cavities for nesting, as well as more frequent use of pesticides, which may have lethal and sublethal effects on solitary bees (Biddinger 2013; Artz and Pitts-Singer 2015; Rundlöf et al. 2015; Sgolastra et al. 2017; Azpiazu et al. 2019). Moreover, by favoring generalist pollinators, a high proportion of MFCs in the landscape may disrupt local plant-pollinator interactions (Diekötter et al. 2010).

80 The observed contrasting relationships between MFCs and solitary bee
81 abundance or reproduction may be due in part to various sources of hetero-
82 geneity in the aforementioned studies, which we aim to control in the current
83 study. First, these studies were performed in a variety of contexts, in terms of
84 landscape structure, farming practices or climate. In order to generalize the
85 actual role of MFCs, we here analyse a unique dataset obtained across a wide
86 range of agro-environmental contexts. Second, to characterize the effects of
87 MFCs, most researchers studied either (1) immediate impacts, wherein MFCs
88 generally attract bees or other pollinators, with sometimes a positive effect
89 on breeding (Holzschuh et al. 2012, Le Féon et al. 2013, and Diekötter et
90 al. 2014) or (2) year-to-year effects, wherein MFCs may influence bee abun-
91 dance the following year (Jauker, Peter, et al. 2012 and Riedinger et al. 2015).
92 Only inter-annual effects of MFCs on the fitness of wild pollinators and their
93 population growth rate would promote their maintenance in the long term.
94 Understanding the balance between positive effects, through the delivery of
95 floral resources, and negative effects, through possible pesticide contamina-
96 tion, according to agro-environmental contexts is necessary to inform future
97 agro-ecological management of these crops.

98 This study investigates the relationship between the reproduction of cavity-
99 nesting pollinators (solitary bees, but also wasps) and mass-flowering crop
100 cover over a whole country. Our goal is to complement previous studies, on
101 the one hand by examining year-to-year effects to assess the long term impact
102 of MFCs, and on the other hand by considering a broad area and a variety of
103 contexts. Our originality is to rely on a citizen science program with a large
104 number of sites (nearly 600 fields) all over France. We focus on immediate
105 and year-to-year landscape correlations with bee or wasp reproduction. We
106 aimed to assess whether the cover of two widespread MFCs (rapeseed and
107 sunflower) was correlated with solitary bee and wasp nesting both in the year
108 of monitoring and in the following year, and thus might be able to support
109 pollinator populations through time.

110 2 Material and methods

111 2.1 Participatory monitoring of solitary bees in field edges

112 The study was conducted in fields monitored by farmers all over mainland
113 France between 2012 and 2017, within the framework of the Farmland Bio-
114 diversity Observatory (FBO). The FBO targets several taxonomic groups to
115 identify farming practices and landscape elements that promote farmland bio-
116 diversity (Billaud, Vermeersch, and Porcher 2020). To our knowledge, this is
117 one of the first national biodiversity monitoring programs to use a participa-
118 tory approach involving farmers. Over a total of 1,501 sites, we selected 576
119 sites, including 416 field crops and 166 meadows, for which all required envi-
120 ronmental variables (see below), including geographical coordinates, were well

121 reported. Some sites were monitored several years in a row (see below for more
122 details).

123 2.2 Trap nests in field boundary

124 All farmers set up two standardized trap nests 5 meter away from each other
125 in each studied field boundary. A trap nest consisted of 32 cardboard tubes
126 that were fixed facing south, on a wooden post, 1 meter above the ground
127 (Billaud, Vermeersch, and Porcher 2020). Farmers monitored nest occupancy,
128 an indicator for reproductive performance, by counting sealed tubes. They also
129 reported a proxy for the diversity of nesting species by identifying the sealing
130 material (mud, chewed leaves, trichomes of woolly plants...). Theoretically,
131 trap nests were meant to be monitored once a month between March and
132 November, but some observers tended to forget some of the surveys. Within a
133 year, 91.8% of sites were sampled at least twice, and 49% at least five times.
134 Accordingly, we did not summarize data within a year, but chose to use all
135 3,345 observations, i.e. one count in a given month per trap nest. Note, how-
136 ever, that other analysis choices, such as considering the maximum number of
137 sealed tubes within a year, did not modify the main results (not shown).

138 We focused our study on both total abundance (pooling all sealing ma-
139 terials) and abundance of the most abundant category of sealing material,
140 i.e. mud, which represents 65% of observations. These mud-sealed tubes are
141 likely to be made in great part by *Osmia* bees (Linsley 1958), which are early
142 spring foragers. We therefore expect them to benefit more from the presence
143 of rapeseed than from that of sunflower. However, this prediction should be
144 considered with caution because other cavity-nesting, flower-visiting taxa such
145 as some *Megachile* (e.g. subgenus *Chalicodoma*, see Michener 2007), and soli-
146 tary wasps such as *Eumeninae*, *Sphecidae* and *Crabronidae* (Steffan-Dewenter
147 and Leschke 2003; Pereira-Peixoto et al. 2014; MacIvor and Packer 2015), may
148 also use mud for nest building.

149 2.3 Environmental variables

150 *Landscape variables* We used the national cartographic field registry (*Registre*
151 *parcellaire graphique*, RPG) to map each crop type within a buffer around
152 each study site. We chose the size of the buffer *a priori* on the basis of ecolog-
153 ical knowledge of solitary bees instead of testing multiple spatial extents and
154 taking the one that best predicts the response, because the latter approach
155 is sometimes biased (Jackson and Fahrig 2015). The area of each crop in the
156 buffer was calculated using the R package *sf* (Pebesma 2018).

157 We computed the area of the two main MFCs (rapeseed and sunflower)
158 both in the sampling year and the previous year. For the sampling year cal-
159 culation, we used a 250m-radius buffer since the distance at which half of the
160 population discontinues foraging (few hundred meters) is more relevant than

161 the species specific maximum foraging distance (Zurbuchen et al. 2010). For
162 the previous year calculation, we decided to use a 1000m-radius buffer because
163 the dispersal distance, from the emergence site to the nesting site, is larger
164 than the median foraging distance of solitary bees and wasps. We chose the
165 buffer sizes according to the measurements by Zurbuchen et al. (2010) for two
166 species of the *Osmiini* tribe with different sizes (*Hylaeus punctulatissimus* and
167 *Hoplitis adunca*), as a proxy for the foraging and dispersal distances of all pol-
168 linators visiting the trap nests. However, the choice of the buffer radius (250m
169 or 1,000m) for the area of MFCs the year preceding the observation did not
170 influence the results (not shown).

171 In order to take into account all other floral resources beyond crops and
172 nesting opportunities, we also computed the area of temporary meadows for
173 both sampling year and previous year and the area of orchards and perma-
174 nent meadows in the sampling year only (because these land uses change little
175 through time). We followed the definition of the Common Agricultural Policy
176 of the European Union to differentiate permanent (5 years or more) vs. tem-
177 porary meadows (≤ 4 years). Finally, as forest margins are known to influence
178 wild bees (Bailey et al. 2014; Joshi et al. 2016; Odanaka and Rehan 2020),
179 we also computed the perimeter of forests in the buffer using the Corine Land
180 Cover database provided by the European Environmental Agency.

181 *Local variables* For each field, farmers reported the presence of surrounding
182 linear elements: hedgerows and their age (old vs. young, a qualitative assess-
183 ment at the discretion of the observer), grass strips, roads, ditches, woody
184 margins. They were used in the models below to inform on potential food
185 sources next to the trap nests. We characterized farming practices with two
186 classes on the basis of farmers' reporting. For nesting observations located in
187 a meadow edge, we used the type of meadow (temporary vs. permanent). For
188 nesting observations located in a field crop edge, we used the farming system
189 (conventional vs. organic farming).

190 *Control variables* We assessed local weather conditions with the E-OBS database
191 from the European Climate Assessment Dataset project (Cornés et al. 2018).
192 Spring weather conditions influence the phenology of early solitary bees and
193 wasps that can forage on rapeseed (Vicens and Bosch 2000), on the one hand,
194 and the flowering period of rapeseed and the sowing date of sunflower, on the
195 other hand. For each monitored field, we chose to compute the mean temper-
196 ature and the sum of precipitation between the 20th of February and either
197 the 31st of May or the sampling date, whichever came first. Since we did not
198 know the exact nest installation date, we also included the number of days
199 between the beginning of the year and the observation date as a proxy for the
200 period of time during which a nest is installed. These three variables (mean
201 temperature, sum of precipitation and time) were included in the model be-
202 low as control variables, i.e. we checked that their effect was consistent with
203 expectations.

204 2.4 Statistical analysis

205 The correlations between landscape resources and the presence/absence and
 206 abundance of sealed tubes in trap nests were assessed using two hurdle mixed
 207 models, one for each field edge type (field crop and meadow), in R (R Core
 208 Team 2020) on RStudio (RStudio Team 2019) with the *glmmTMB* package
 209 (Brooks et al. 2017). Hurdle models are two-stage models that provide a way
 210 of modeling the excessive proportion of zero values and are known to perform
 211 well for ecological data (Potts and Elith 2006). The first stage models the
 212 presence/absence of sealed tubes with a probability of presence π , and the
 213 second stage models their abundance, with mean μ , conditional on the pres-
 214 ence of mud-sealed tubes. Compared to zero-inflation models, a hurdle model
 215 assumes that there is a single process by which a zero can be produced.

216 Let $Y_{i,j,k}$ be a random variable that represents the number of sealed tubes
 217 observed during the k^{th} observation in plot j of year i . The hurdle mixed
 218 model is the following:

$$\Pr\{Y_{i,j,k} = y | \pi_{i,j,k}, (\theta, \mu_{i,j,k})\} = \begin{cases} 1 - \pi_{i,j,k}, & y = 0 \\ \pi_{i,j,k} \frac{NegBin\{y, (\theta, \mu_{i,j,k})\}}{1 - NegBin\{0, (\theta, \mu_{i,j,k})\}}, & y > 0 \end{cases}$$

$$\text{logit}(\Pi) = X_{zero} * B_{zero} + S_{zero} \quad \text{logit}(M) = X_{count} * B_{count} + S_{count}$$

219 with Π and M vectors of probabilities $\pi_{i,j,k}$ and means $\mu_{i,j,k}$, X_{zero} and
 220 X_{count} vectors of fixed effects listed in Appendix A with their related vectors
 221 of coefficients B_{zero} and B_{count} , S_{zero} (resp S_{count}) the vector of site ran-
 222 dom intercepts $s_j^{zero} \sim \mathcal{N}(0, \sigma_{zero}^2)$ (resp. $s_j^{count} \sim \mathcal{N}(0, \sigma_{count}^2)$), and θ the
 223 dispersion parameter of the negative binomial.

224 In our models, we included five types of variables with fixed effects, which
 225 are listed in Appendix A: (1) four variables related to the quantity of floral re-
 226 sources provided by MFCs (area of rapeseed and sunflower in the current and
 227 previous year), (2) seven variables related to the semi-natural elements likely to
 228 provide additional floral resources and nesting opportunities in the surround-
 229 ing landscape, (3) eight variables describing either local practices in the field
 230 neighbouring the monitoring site or local food/nesting sources and (4) their in-
 231 teractions with landscape resources, and finally (5) three control variables. We
 232 also included a site random effect to take into account the non-independence
 233 of repeated observations in some fields, within a year and between years (131
 234 sites were monitored at least two consecutive years). All variables were stan-
 235 dardized and centered. Note that, to avoid multicollinearity issues, we did not
 236 include the type of crop sown in the neighbouring field in the models because
 237 it was indirectly taken into account in the landscape variables.

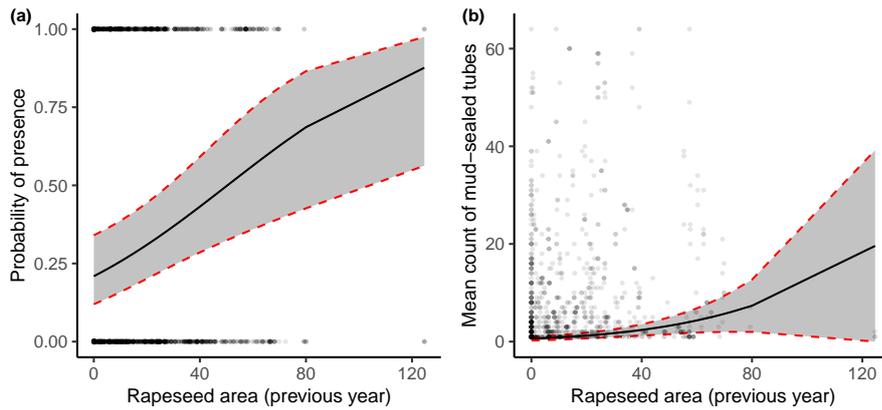


Fig. 1 Relationship between (a) probability of presence of a mud-sealed tube or (b) abundance of mud-sealed tubes, in trap nests set up in field crop edges, and rapeseed field area in the previous year. Continuous black lines are either (a) the predicted zero-inflation probability or (b) the mean model prediction conditioned on the fixed effects and the zero-inflation component. Grey ribbons are the confidence intervals. Each grey point represents one observation; multiple grey points on top of each other appear in darker grey.

238 We first analysed full models (see Appendix A). Then, we ran an automatic
 239 selection with the R package *MuMIn* (Bartoń 2020), using the corrected
 240 Akaike information criteria (AICc) and fixing several variables of interest for
 241 our main questions. Variables selected through this process are in italics in
 242 Table 1. We also checked the variance inflation factor with the R package *per-*
 243 *formance* (Lüdecke et al. 2020) to ensure there was no multicollinearity (see
 244 Appendix B). We used the *DHARMA* package (Hartig 2020) for residual diag-
 245 nostics. Residual overdispersion and zero-inflation were acceptable upon visual
 246 inspection (see Appendix C). The Durbin-Watson test was not significant for
 247 most of the residuals, we thus decided to ignore temporal autocorrelation (see
 248 Appendix D).

249 Model outputs were formatted with the help of the *texreg* package (Leifeld
 250 2013). Finally, we used the *ggeffects* package (Lüdecke 2018) to build output
 251 figures.

252 This workflow of data analysis was applied to two dependent variables :
 253 the number of mud-sealed tubes, representing the majority of observations,
 254 and the total number of sealed tubes. In the following, we present mostly
 255 results on mud-sealed tubes, because they are generally similar to results for
 256 all tubes and because they are likely to represent patterns for a more restricted
 257 taxonomic group. We nonetheless discuss dissimilarities between both analyses
 258 and provide full results on all tubes in Appendix E.

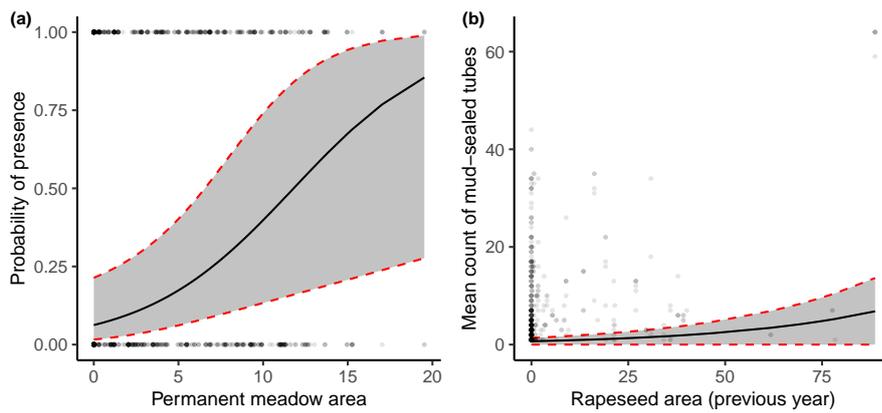


Fig. 2 Relationship between (a) probability of presence of a mud-sealed tube and permanent meadow area, or (b) abundance of mud-sealed tubes and rapeseed field area in the previous year, in trap nests set up in meadow edges. Continuous black lines are either (a) the predicted zero-inflation probability or (b) the mean model prediction conditioned on the fixed effects and the zero-inflation component. Grey ribbons are the confidence intervals. Each grey point represents one observation; multiple grey points on top of each other appear in darker grey.

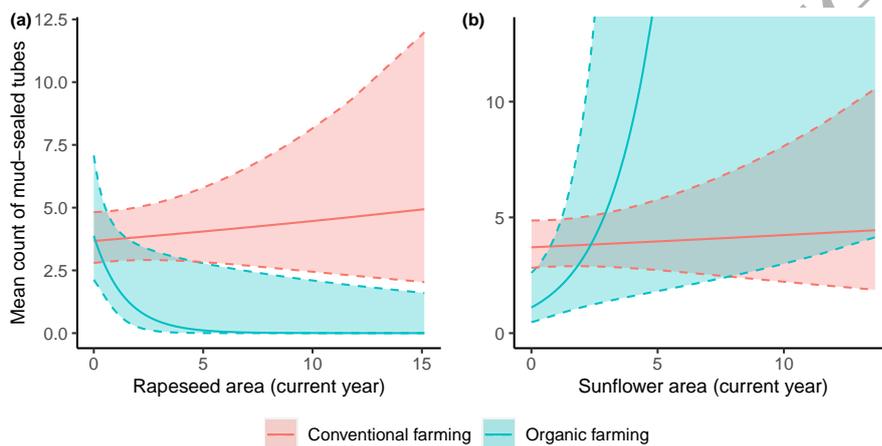


Fig. 3 Relationship between abundance of mud-sealed tubes and mass-flowering crop area ((a) rapeseed, or (b) sunflower), for trap nests set up in field crop edges across different farming systems. Lines are the mean model predictions, conditioned on the fixed effects and the zero-inflation component. Ribbons are the confidence intervals.

Table 1 Output of hurdle models examining the relationship between the presence of mud-sealed tubes ("Zero model") or their abundance conditional on presence ("Count model") and environmental variables. The table shows the parameter estimates, with standard errors in parentheses, after automatic selection of variables. Non-italicized variables were fixed, while italicized variables are those that were retained during the automatic selection process. Parameters with a p-value < 0.05 are highlighted in bold. All variables were standardized and centered.

	Zero model		Count model	
	Field crops	Meadows	Field crops	Meadows
Intercept (conventional farming, no landscape elements nearby)	-0.90 (0.30)**		1.32 (0.14)***	
Intercept (temporary meadow, no landscape elements nearby)		-1.72 (0.59)**		1.63 (0.20)***
Landscape variables				
Area of rapeseed (current year)	-0.14 (0.11)	0.31 (0.20)	0.04 (0.06)	-0.04 (0.06)
Area of rapeseed (previous year)	0.50 (0.15)***	0.13 (0.29)	0.31 (0.09)***	0.24 (0.09)**
Area of sunflower (current year)	-0.07 (0.12)	-0.35 (0.30)	0.03 (0.07)	0.10 (0.16)
Area of sunflower (previous year)	-0.41 (0.17)*	-0.16 (0.38)	-0.04 (0.09)	-0.10 (0.16)
Area of permanent meadows	0.69 (0.19)***	1.03 (0.38)**	0.27 (0.09)**	0.11 (0.11)
<i>Area of temporary meadows (current year)</i>		1.15 (0.46)*		-0.40 (0.16)*
<i>Area of temporary meadows (previous year)</i>		-1.09 (0.49)*		0.30 (0.15)*
<i>Perimeter of forests</i>	0.37 (0.19)*			
Local variables				
Organic farming	0.48 (0.57)		-0.75 (0.43)	
Permanent meadow		0.51 (0.40)		-0.01 (0.18)
<i>Road</i>	-0.68 (0.31)*			-0.50 (0.20)*
<i>Young hedgerow</i>		1.16 (0.66)		
<i>Old hedgerow</i>	0.59 (0.31)	0.41 (0.62)	-0.14 (0.18)	
Interactions				
Area of rapeseed (cur. year):Organic farming	-0.33 (0.82)		-1.51 (0.70)*	
Area of rapeseed (prev. year):Organic farming	0.72 (0.70)		-0.31 (0.31)	
Area of sunflower (cur. year):Organic farming	-0.27 (0.41)		1.03 (0.46)*	
Area of sunflower (prev. year):Organic farming	-0.79 (0.52)		0.19 (0.28)	
Area of permanent meadows:Organic farming	-0.30 (0.59)		-0.07 (0.28)	
Control variables				
Temperature	1.32 (0.14)***	1.79 (0.29)***	0.40 (0.07)***	0.24 (0.10)*
Precipitation	0.66 (0.11)***	1.44 (0.26)***	0.37 (0.05)***	0.25 (0.09)**
Number of days	0.60 (0.09)***	1.07 (0.16)***	0.02 (0.04)	0.18 (0.06)**
Variance of site random effect	8.69	14.95	1.88	0.93

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Field crops : trap nests set up in field crop edges ; Meadows : trap nests set up in meadow edges

259 3 Results

260 3.1 Relationship between area of mass-flowering crops and reproduction of 261 cavity-nesting pollinators

262 Nesting was generally positively correlated with the quantity of floral resources
263 provided by MFCs, but the relationships depended on the type of sealing material,
264 the identity of crops and the timing of resource availability. For rapeseed,
265 only the area cultivated the year preceding observations was related to nesting
266 (Table 1, *area of rapeseed (previous year)*). Regardless of the dependent variable,
267 the area of rapeseed fields in the previous year was positively linked to

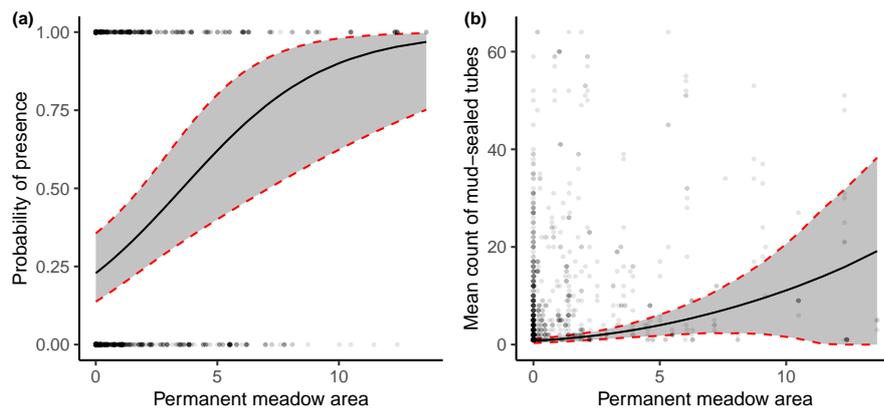


Fig. 4 Relationship between (a) probability of presence of a mud-sealed tube or (b) abundance of mud-sealed tubes, in trap nests set up in field crop edges, and permanent meadow area. Continuous black lines are either (a) the predicted zero-inflation probability or (b) the mean model prediction conditioned on the fixed effects and the zero-inflation component. Grey ribbons are the confidence intervals. Each grey point represents one observation; multiple grey points on top of each other appear in darker grey.

268 the abundance of occupied tubes in field crop edges (Fig. 1b) and in meadow
 269 edges (Fig. 2b). The area of rapeseed fields in the previous year was also posi-
 270 tively related to the presence of mud-sealed tubes in field crop edges (Fig. 1a).
 271 In contrast, the area of rapeseed fields in the current year did not correlate
 272 significantly with pollinator nesting, regardless of the model (Table 1, *area*
 273 *of rapeseed (current year)*). For sunflower, field area in the previous year was
 274 negatively linked to the presence of mud-sealed tubes in field crop edges, but
 275 the area of sunflower fields in the year of observations was positively related
 276 to the presence of all types of sealing materials (Table 1, *area of sunflower*
 277 *(previous year)* and Appendix E, Table 4, *area of sunflower (current year)*).
 278 Similarly, in meadow edges sunflower area was positively related to the pres-
 279 ence of occupied tubes (Appendix E, Table 4). In all other cases, there was no
 280 significant correlation of sunflower area with bee and wasp reproduction.

281 In addition to the simple effect of previous year MFC area on mud-sealed
 282 tubes, we observed significant interactions of current-year MFC area with the
 283 farming system, although the latter did not have a significant simple effect
 284 (Table 1, *area of rapeseed (cur. year):organic farming* and *area of sunflower*
 285 *(cur. year):organic farming*). These interactions differed between MFCs. With
 286 rapeseed, the relationship between mud-sealed tube abundance and coexisting
 287 crop area varied from slightly positive to negative in conventional vs. organic
 288 fields (Fig. 3a). In contrast, with sunflower, the same relationship varied from
 289 slightly positive to strongly positive in conventional vs. organic fields (Fig. 3b).
 290 The significance of these interactions were however sensitive to the dependent
 291 variable considered (Tables 4 and 5 in Appendix E).

292 3.2 Relationship between other landscape elements and reproduction of 293 cavity-nesting pollinators

294 The presence and abundance of mud-sealed tubes also correlated significantly
295 with the area of semi-natural elements likely to provide food or nesting sources
296 (Table 1, *area of permanent meadows*). Both presence and abundance of oc-
297 cupied tubes were positively correlated with the area of permanent meadows
298 in field crop edge (Fig. 4), regardless of the dependent variable. Similarly, in
299 meadow edges, the presence of occupied tubes, but not their abundance, was
300 positively linked to permanent meadow area (Fig. 2a). Temporary meadows
301 had more variable relationships with solitary bee and wasp reproduction. In
302 meadow edges, temporary meadow area in the current year was positively re-
303 lated to the presence of mud-sealed tubes, but this area in the previous year was
304 negatively related to the presence of mud-sealed tubes (Zero model in Table 1,
305 *area of temporary meadows*). The pattern was opposite for abundance (Count
306 model in Table 1, *area of temporary meadows*). These relationships were not
307 significant in models considering the maximum number of mud-sealed tubes
308 or all occupied tubes (Table 4, Appendix E). The presence of occupied tubes
309 was generally positively related to perimeter of forests in field crop edge, but
310 the presence of hedgerows had no detectable correlation in any model. The
311 proximity of a road was negatively related to the abundance of occupied tubes
312 in meadow edges, and to the presence of occupied tubes in field crop edges.
313 Finally, the type of meadow was not significantly correlated with nesting mea-
314 sured in meadow edges.

315 3.3 Control variables

316 In all models, the number of days since the beginning of the year was positively
317 related to the presence of mud-sealed tubes. Similarly, when significant, mean
318 temperature and sum of precipitation correlated positively with both presence
319 and abundance of mud-sealed tubes.

320 4 Discussion

321 While examining the landscape and local correlates of solitary bee and wasp
322 nest building across a whole country, we observed positive relationships with
323 the area of landscape elements that provide resources, i.e. rapeseed, sunflower
324 and permanent meadows. For rapeseed, this relationship was true only for
325 the area cultivated the year preceding observations, regardless of the tube-
326 sealing material considered. For sunflower, nesting was positively linked with
327 crop area in the current year when all sealing materials were considered, but
328 negatively linked with crop area in the previous year when considering mud-
329 sealed tubes only. In the following we discuss the implications of our findings
330 for the management of agricultural landscapes.

331 4.1 Inter-annual impacts of mass flowering crops on nest building in solitary 332 bees and wasps

333 We focused our study on the inter-annual effects of landscape floral resources
334 on the reproduction of wild bees and wasps. We evidenced a positive corre-
335 lation between rapeseed field area in the previous year and solitary bee and
336 wasp nesting, both in the zero model and the abundance model. Such correla-
337 tion suggests that rapeseed may have a lasting year-to-year impact on bee and
338 wasp reproduction. Whereas solitary bee nest-building was previously shown
339 to increase during the period of mass-flowering (Jauker, Peter, et al. 2012), we
340 did not find any significant impact of the area of rapeseed of the current year.
341 Our results indicate that the previous year resources seem to benefit more
342 to nest-building and thus to support production of sexuals, a requirement to
343 carry over benefits into the next season.

344 The next-year positive effect of rapeseed floral resources may be related
345 to nest provisioning. Although both males and females feed on flowers, only
346 females invest in brood care. During spring, solitary bee and wasp females
347 collect building materials and food for the nest, where the eggs are laid in in-
348 dividual cells. The larvae stay in the nest throughout the summer and winter,
349 using pollen reserves, and emerge the following spring. Reproductive success
350 thus depends on the female's ability to provision nests with enough pollen
351 mixture to ensure the emergence of enough offspring the following year. Trap
352 nests only provide information about the number of sealed tubes, and not
353 about the actual number of cells and larvae in each tube. We do not know
354 the actual number of viable offspring that will emerge the following spring: in
355 previous studies, it has been shown that sometimes no adults emerge from a
356 nest, notably because all cells can be parasitized (e.g. Steffan-Dewenter 2002).
357 Variation in offspring number within sealed tubes may explain the contrasting
358 correlations of bee and wasp reproduction with previous year and current year
359 rapeseed cover. Available floral resources during breeding season allow each
360 female to lay more eggs in each tube, and to provision more pollen mixture for
361 each larvae, which will result in a higher abundance in the next year, hence
362 in a positive correlation between nesting and previous year rapeseed cover.
363 However, females may not necessarily seal more tubes even when more pollen
364 resources are available because of the high cost of the nest plug (Rust 1993),
365 hence the non-significant effect of current rapeseed cover on bee reproduction.
366 Riedinger et al. (2015) showed that rapeseed has a year-to-year effect by pro-
367 moting a higher solitary bee and wasp abundance the following year. Here we
368 show that this higher abundance of solitary bees and wasps, which we did not
369 measure directly, also translates into higher reproductive potential, an indirect
370 piece of evidence that rapeseed promotes solitary bee and wasp populations
371 (Fig. 5). This result was not completely expected, since the rapeseed blooming
372 period is limited, and since its pollen may be of minor importance for larvae
373 diet (Coudrain et al. 2016). Moreover, as a result of crop rotation, a high rape-
374 seed cover one year may lead to a lack of floral resources in the landscape the
375 following year.

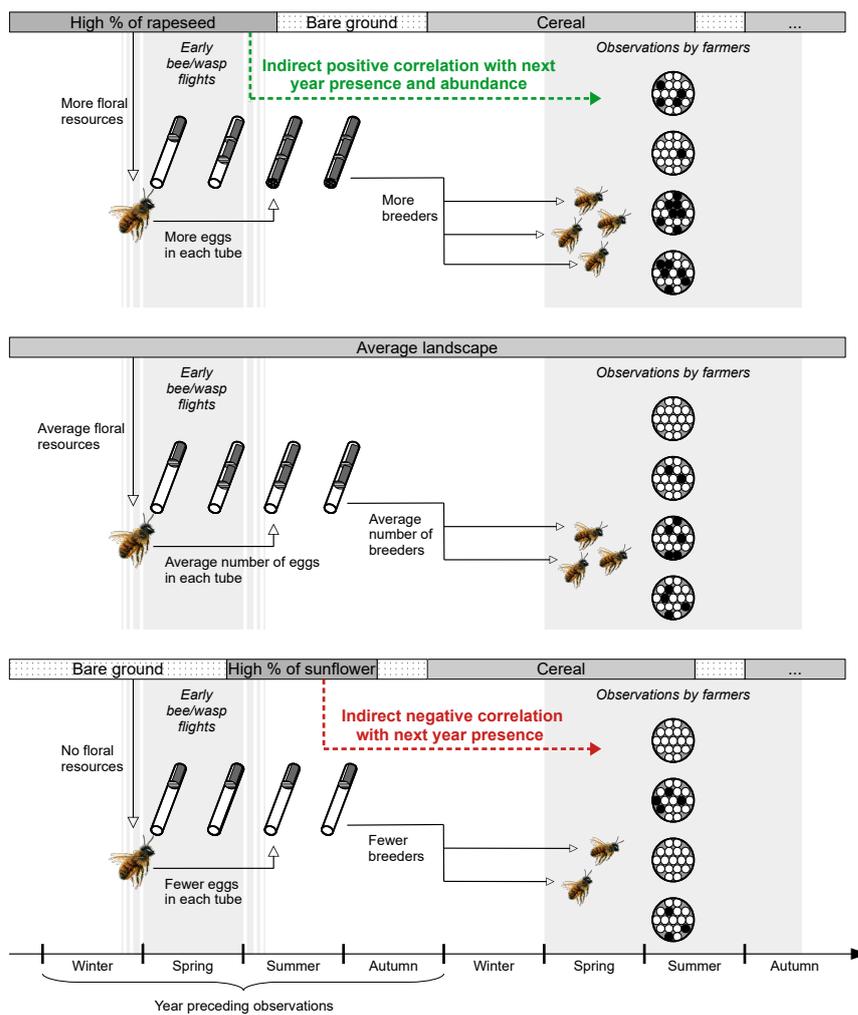


Fig. 5 Schematic summary of possible inter-annual effects of rapeseed (top) or sunflower (bottom) floral resources on solitary bee reproduction, as compared with an average landscape (middle). *Osmia rufa* drawing by Valerie Littlewood, used with permission.

376 Sunflower area had a more contrasting correlation with wild bee/wasp re-
 377 production, depending on the type of sealing material analyzed. For mud-
 378 sealed tubes the relation with previous-year resources was on the whole more
 379 negative than for rapeseed, whereas when counting all tubes the relation with
 380 current-year resources was positive. Unlike rapeseed that blooms in spring,
 381 sunflower is a summer crop. The different relationships with bee reproduction
 382 may confirm that mud-sealed tubes are mainly produced by solitary bees active

383 in early spring, such as *Osmia*, which are known to pollinate spring-blooming
384 crops (Bosch, Sgolastra, and Kemp 2008). Sunflower area was negatively cor-
385 related with next-year reproduction of pollinators using mud in the presence
386 model in field crop edges. This negative correlation between sunflower field
387 area in the previous year and the presence of mud-sealed nests may be un-
388 derstood according to the same logic of interpretation as the one adopted in
389 the case of the effects of rapeseed. Since sunflower is a summer crop sown in
390 April, a high cover leads to a lack of floral resources during the spring and
391 may therefore reduce the number of breeders in the next year (Fig. 5). How-
392 ever, according to this hypothesis, the abundance, not only the presence, of
393 mud-sealed tubes should also have been negatively correlated with sunflower
394 field area in the previous year. Finally the dissimilarities between the effect
395 of sunflower when all tubes vs. mud-sealed tubes only are considered suggest
396 that on average species using sealing materials other than mud have later phe-
397 nologies than species using mud and are positively affected by the resources
398 provided by sunflower. Differences were observed on zero models only probably
399 because mud-sealed tubes represent the majority of observations and drive the
400 abundance data.

401 We found little correlation of bee and wasp reproduction with the area of
402 MFCs growing simultaneously but the interactions between MFC cover in the
403 current year and farming system were sometimes significant, in a surprising
404 way. We expected local pesticide use intensity to have negative effects on nest-
405 ing, and even to counteract the positive effects of MFC floral resources and
406 semi-natural habitats as demonstrated for pest biological control (Ricci et al.
407 2019). Our analyses did not confirm these predictions, since farming system
408 alone did not have any significant effect and conventional practices interacted
409 positively with rapeseed resources (Fig. 3). Besides, some of these significant
410 interactions tended to vanish when studying the total number of occupied
411 nests instead of mud-sealed tubes. Again, these differences are consistent with
412 the hypothesis of partly different spring and summer communities. One reason
413 why we did not observe general negative effects of conventional farming may
414 be related to our data not measuring the number of offspring directly: pesticide
415 exposure might not reduce nesting, but only reduce offspring production and
416 alter the sex-ratio (Stuligross and Williams 2020). However, these results are
417 difficult to interpret because we lack information on practices at the landscape
418 level, while some authors emphasize the need to combine both local and land-
419 scape levels when assessing the impacts of the intensity of farming practices
420 (Carrié et al 2017).

421 4.2 Importance of semi-natural elements and other permanent landscap 422 features

423 Both for the probability of presence and abundance of sealed tubes, the area
424 of permanent meadows in the buffer strongly promoted solitary bee and wasp
425 reproduction. This is consistent with previous studies which showed that loss

of semi-natural habitats, i.e. land uses that are minimally managed and not cultivated for arable crops, is one of the main drivers of pollinator decline (Ricketts et al. 2008; Tscharntke et al. 2012). As the dynamics of wild bee populations are mainly driven by the amount of nesting and floral resources (Lonsdorf et al. 2009), semi-natural areas help maintain bee populations (Carré et al. 2009; Tscharntke et al. 2012) by providing both nesting and food opportunities. Remaining permanent meadows may also be important to offset bee decline caused by meadow-to-crop conversion that occurred long ago (Provost et al. 2020). Moreover, these semi-natural habitats may decrease the negative effect of warmer temperature on bee populations (Papanikolaou et al. 2017) and buffer the harmful impacts of pesticides (Park et al. 2015).

In both our models however, there was no evidence of a positive effect of the proximity of hedgerows, except for the probability of nesting, regardless of sealing material, in field crops. This observation goes against our expectations, since it has been shown that abundance and diversity of wild bees are enhanced in field edges by hedgerows (Morandin and Kremen 2013). This result may be due to the fact that this parameter is reported by farmers, whose definition of a hedgerow may differ and may include different types of vegetation and different stages of the hedgerows (recently planted or older, more or less diversified). By contrast, our models evidenced a negative impact of the presence of a road. The amount of roads has already been shown to decrease bumblebee density (Kallioniemi et al. 2017), but road verges could also provide floral resources for wild bees (Henriksen and Langer 2013).

Semi-natural areas and mass-flowering crops do not have the same relative importance. In both zero models, the area of permanent meadows had a stronger positive effect than the area of rapeseed in the previous year. On the contrary, in both count models, the impact of rapeseed was slightly to substantially stronger. The presence of sealed tubes thus seems to depend more on semi-natural areas while their abundance seems to depend more on the resources provided by rapeseed. Nevertheless, the permanent meadow area does not condition the positive effect of rapeseed: we tested the interaction between the two variables and we did not find any significant correlation (not shown). The presence of permanent meadows may be an important factor when a wild bee chooses where to build its nest, because some wild flowers in meadows are in bloom before rapeseed fields and thus are more attractive. Once the nest is built, rapeseed will provide a massive amount of pollen and nectar to pollinators active during its flowering period (such as *Osmia*), allowing each female to lay more eggs in each tube and thus increasing the number of breeders the following year.

5 Conclusion: implications for pollinator conservation in agricultural landscapes

Defining how agriculturally dominated landscapes can be optimized for wild bees remains a complex subject. Our study shows that solitary bee and wasp

reproduction can be positively and durably affected by rapeseed cover. This crop provides a massive amount of floral resources at a period favorable for early wild bees. Moreover, our study confirms that permanent meadows are essential to promote solitary bee and wasp populations. The positive effect of rapeseed cover may hold only if enough food and nesting sites are available in adjacent natural habitats. Ricketts et al. (2008) showed that flower-visitor richness and visitation rate in croplands decline with distance from natural areas, and a lack of natural habitats can directly impact on crop yield (Garibaldi et al. 2011; Holzschuh et al. 2012). Protecting natural habitats near crop fields seems to be a key solution to secure natural supply of pollination service, and moderate covers of rapeseed may help to maintain solitary bee populations. However, rapeseed flowering period is short, thus pollinators still need floral resources from other crops and other semi-natural habitats (Martins et al. 2018), especially as we studied a small part of the solitary bee and wasp community. The use of rapeseed for promoting wild pollinators needs also to be viewed bearing in mind the heavy pesticide application on this crop.

Acknowledgments

We thank all farmers who provided observations from their fields, the FBO management team (Elodie Chauvet, Marion Demade, Marie Garnier, Marine Gérardin, Romain Julliard, Christophe Pinard, Nora Rouillier and Rose-Line Vermeersch) and the French Ministry of Agriculture, which supported the program. We also thank Adrien Perrard and three anonymous reviewers for their insightful comments and for shedding some light on the diversity of potential trap nest residents.

Declarations

Funding This research project was funded by the Crédit Agricole through sponsoring to O.B. and V.V.

Conflicts of interest All authors declare that they have no conflict of interests.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Availability of data The data associated with this study will be available on Zenodo upon acceptance of the manuscript.

Code availability The R code used for statistical analyses will be made available on GitHub upon acceptance of the manuscript.

504 *Authors' contributions* All authors contributed to the study conception and
505 design. Data collection and analysis were performed by Victor Van der Meersch
506 and Olivier Billaud. The first draft of the manuscript was written by Victor
507 Van der Meersch and Emmanuelle Porcher, and all authors commented on
508 previous versions of the manuscript. All authors read and approved the final
509 manuscript.

510 References

- 511 Artz, Derek R., and Theresa L. Pitts-Singer. 2015. "Effects of Fungicide and
512 Adjuvant Sprays on Nesting Behavior in Two Managed Solitary Bees, *Osmia*
513 *Lignaria* and *Megachile Rotundata*." Edited by Nicolas Desneux. *PLOS ONE*
514 10 (8): e0135688. <https://doi.org/10.1371/journal.pone.0135688>.
- 515 Azpiazu, Celeste, Jordi Bosch, Elisa Viñuela, Piotr Medrzycki, Dariusz
516 Teper, and Fabio Sgolastra. 2019. "Chronic Oral Exposure to Field-Realistic
517 Pesticide Combinations via Pollen and Nectar: Effects on Feeding and Thermal
518 Performance in a Solitary Bee." *Scientific Reports* 9 (1). <https://doi.org/10.1038/s41598-019-50255-4>.
- 520 Bailey, Samantha, Fabrice Requier, Benoit Nusillard, Stuart P. M. Roberts,
521 Simon G. Potts, and Christophe Bouget. 2014. "Distance from Forest Edge
522 Affects Bee Pollinators in Oilseed Rape Fields." *Ecology and Evolution* 4 (4):
523 370–80. <https://doi.org/10.1002/ece3.924>.
- 524 Bartoń, Kamil. 2020. *MuMIn: Multi-Model Inference*. [https://CRAN.R-](https://CRAN.R-project.org/package=MumIn)
525 [project.org/package=MumIn](https://CRAN.R-project.org/package=MumIn).
- 526 Benton, Tim G., David M. Bryant, Lorna Cole, and Humphrey Q. P. Crick.
527 2002. "Linking Agricultural Practice to Insect and Bird Populations: A His-
528 torical Study over Three Decades." *Journal of Applied Ecology* 39 (4): 673–87.
529 <https://doi.org/10.1046/j.1365-2664.2002.00745.x>.
- 530 Biddinger, Jacqueline L. AND Mullin, David J. AND Robertson. 2013.
531 "Comparative Toxicities and Synergism of Apple Orchard Pesticides to *Apis*
532 *Mellifera* (L.) and *Osmia Cornifrons* (Radoszkowski)." *PLOS ONE* 8 (9): 1–6.
533 <https://doi.org/10.1371/journal.pone.0072587>.
- 534 Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards,
535 T. Peeters, A. P. Schaffers, et al. 2006. "Parallel Declines in Pollinators and
536 Insect-Pollinated Plants in Britain and the Netherlands." *Science* 313 (5785):
537 351–54. <https://doi.org/10.1126/science.1127863>.
- 538 Billaud, Olivier, Rose-Line Vermeersch, and Emmanuelle Porcher. 2020.
539 "Citizen Science Involving Farmers as a Means to Document Temporal Trends
540 in Farmland Biodiversity and Relate Them to Agricultural Practices." *Journal*
541 *of Applied Ecology*. <https://doi.org/10.1111/1365-2664.13746>.
- 542 Bosch, Jordi, Fabio Sgolastra, and William P. Kemp. 2008. "6. Life Cycle
543 Ecophysiology of *Osmia* Mason Bees Used as Crop Pollinators." In *Bee Polli-*
544 *nation in Agricultural Eco-Systems*, 83–105. Oxford University Press. [https:](https://doi.org/10.1093/acprof:oso/9780195316957.003.0006)
545 [//doi.org/10.1093/acprof:oso/9780195316957.003.0006](https://doi.org/10.1093/acprof:oso/9780195316957.003.0006).

- 546 Bretagnolle, Vincent, and Sabrina Gaba. 2015. "Weeds for Bees? A Re-
547 view." *Agronomy for Sustainable Development* 35 (3): 891–909. <https://doi.org/10.1007/s13593-015-0302-5>.
- 549 Brooks, Mollie E., Kasper Kristensen, Koen J. van Benthem, Arni Mag-
550 nusson, Casper W. Berg, Anders Nielsen, Hans J. Skaug, Martin Maechler,
551 and Benjamin M. Bolker. 2017. "glmmTMB Balances Speed and Flexibility
552 Among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *The*
553 *R Journal* 9 (2): 378–400. [https://journal.r-project.org/archive/2017/
554 RJ-2017-066/index.html](https://journal.r-project.org/archive/2017/RJ-2017-066/index.html).
- 555 Burkle, Laura A., John C. Marlin, and Tiffany M. Knight. 2013. "Plant-
556 Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and
557 Function." *Science* 339 (6127): 1611–5. [https://doi.org/10.1126/science.
558 1232728](https://doi.org/10.1126/science.1232728).
- 559 Carré, Gabriel, Philip Roche, Rémy Chifflet, Nicolas Morison, Riccardo
560 Bommarco, Jenn Harrison-Cripps, Kristin Krewenka, et al. 2009. "Landscape
561 Context and Habitat Type as Drivers of Bee Diversity in European Annual
562 Crops." *Agriculture, Ecosystems and Environment* 133 (1): 40–47. [https://
563 doi.org/https://doi.org/10.1016/j.agee.2009.05.001](https://doi.org/https://doi.org/10.1016/j.agee.2009.05.001).
- 564 Carrié, Romain, Andrieu, Emilie, Ouin, Annie and Steffan-Dewenter, In-
565 golf. 2017. "Interactive effects of landscape-wide intensity of farming practices
566 and landscape complexity on wild bee diversity." *Landscape Ecology* 32: 1631–
567 1642. <https://doi.org/10.1007/s10980-017-0530-y>.
- 568 Carrié, Romain, Johan Ekroos, and Henrik G. Smith. 2018. "Organic Farm-
569 ing Supports Spatiotemporal Stability in Species Richness of Bumblebees and
570 Butterflies." *Biological Conservation* 227: 48–55. [https://doi.org/https://
571 //doi.org/10.1016/j.biocon.2018.08.022](https://doi.org/https://doi.org/10.1016/j.biocon.2018.08.022).
- 572 Cornes, Richard C., Gerard van der Schrier, Else J. M. van den Besselaar,
573 and Philip D. Jones. 2018. "An Ensemble Version of the E-Obs Temperature
574 and Precipitation Data Sets." *Journal of Geophysical Research: Atmospheres*
575 123 (17): 9391–9409. <https://doi.org/10.1029/2017JD028200>.
- 576 Coudrain, Valérie, Sarah Rittiner, Felix Herzog, Willy Tinner, and Martin
577 H. Entling. 2016. "Landscape Distribution of Food and Nesting Sites Affect
578 Larval Diet and Nest Size, but Not Abundance of *Osmia Bicornis*." *Insect*
579 *Science* 23 (5): 746–53. <https://doi.org/10.1111/1744-7917.12238>.
- 580 Diekötter, Tim, Taku Kadoya, Franziska Peter, Volkmar Wolters, and
581 Frank Jauker. 2010. "Oilseed Rape Crops Distort Plant–Pollinator Interac-
582 tions." *Journal of Applied Ecology* 47 (1): 209–14. [https://doi.org/https://
583 //doi.org/10.1111/j.1365-2664.2009.01759.x](https://doi.org/https://doi.org/10.1111/j.1365-2664.2009.01759.x).
- 584 Diekötter, Tim, Franziska Peter, Birgit Jauker, Volkmar Wolters, and Frank
585 Jauker. 2014. "Mass-Flowering Crops Increase Richness of Cavity-Nesting Bees
586 and Wasps in Modern Agro-Ecosystems." *GCB Bioenergy* 6 (3): 219–26. [https://
587 //doi.org/10.1111/gcbb.12080](https://doi.org/10.1111/gcbb.12080).
- 588 Garibaldi, Lucas A, Luísa G Carvalheiro, Sara D Leonhardt, Marcelo A
589 Aizen, Brett R Blaauw, Rufus Isaacs, Michael Kuhlmann, et al. 2014. "From
590 Research to Action: Enhancing Crop Yield Through Wild Pollinators." *Fron-*

591 *tiers in Ecology and the Environment* 12 (8): 439–47. <https://doi.org/10.1890/130330>.

593 Garibaldi, Lucas A., Ingolf Steffan-Dewenter, Claire Kremen, Juan M.
594 Morales, Riccardo Bommarco, Saul A. Cunningham, Luísa G. Carvalheiro,
595 et al. 2011. “Stability of Pollination Services Decreases with Isolation from
596 Natural Areas Despite Honey Bee Visits.” *Ecology Letters* 14 (10): 1062–72.
597 <https://doi.org/10.1111/j.1461-0248.2011.01669.x>.

598 Goulson, D., G. C. Lye, and B. Darvill. 2008. “Decline and Conservation
599 of Bumble Bees.” *Annual Review of Entomology* 53 (1): 191–208. <https://doi.org/10.1146/annurev.ento.53.103106.093454>.

601 Hartig, Florian. 2020. *DHARMA: Residual Diagnostics for Hierarchical*
602 *(Multi-Level / Mixed) Regression Models*. [https://CRAN.R-project.org/package=](https://CRAN.R-project.org/package=DHARMA)
603 *DHARMA*.

604 Henriksen, Casper Ingerslev, and Vibeke Langer. 2013. “Road Verges and
605 Winter Wheat Fields as Resources for Wild Bees in Agricultural Landscapes.”
606 *Agriculture, Ecosystems & Environment* 173: 66–71. <https://doi.org/https://doi.org/10.1016/j.agee.2013.04.008>.

608 Holzschuh, Andrea, Matteo Dainese, Juan P. González-Varo, Sonja Mudri-
609 Stojnić, Verena Riedinger, Maj Rundlöf, Jeroen Scheper, et al. 2016. “Mass-
610 Flowering Crops Dilute Pollinator Abundance in Agricultural Landscapes Across
611 Europe.” *Ecology Letters* 19 (10): 1228–36. <https://doi.org/10.1111/ele.12657>.

613 Holzschuh, Andrea, Carsten F. Dormann, Teja Tscharntke, and Ingolf
614 Steffan-Dewenter. 2012. “Mass-Flowering Crops Enhance Wild Bee Abun-
615 dance.” *Oecologia* 172 (2): 477–84. [https://doi.org/10.1007/s00442-012-](https://doi.org/10.1007/s00442-012-2515-5)
616 *2515-5*.

617 Jackson, Heather Bird, and Lenore Fahrig. 2015. “Are Ecologists Conduct-
618 ing Research at the Optimal Scale?” *Global Ecology and Biogeography* 24 (1):
619 52–63. <https://doi.org/10.1111/geb.12233>.

620 Jauker, Frank, Birgit Bondarenko, Heiko C. Becker, and Ingolf Steffan-
621 Dewenter. 2012. “Pollination Efficiency of Wild Bees and Hoverflies Provided
622 to Oilseed Rape.” *Agricultural and Forest Entomology* 14 (1): 81–87. <https://doi.org/10.1111/j.1461-9563.2011.00541.x>.

624 Jauker, Frank, Franziska Peter, Volkmar Wolters, and Tim Diekötter. 2012.
625 “Early Reproductive Benefits of Mass-Flowering Crops to the Solitary Bee *Os-*
626 *mia Rufa* Outbalance Post-Flowering Disadvantages.” *Basic and Applied Ecol-*
627 *ogy* 13 (3): 268–76. [https://doi.org/https://doi.org/10.1016/j.baee.](https://doi.org/https://doi.org/10.1016/j.baee.2012.03.010)
628 *2012.03.010*.

629 Joshi, Neelendra K., Mark Otieno, Edwin G. Rajotte, Shelby J. Fleischer,
630 and David J. Biddinger. 2016. “Proximity to Woodland and Landscape Struc-
631 ture Drives Pollinator Visitation in Apple Orchard Ecosystem.” *Frontiers in*
632 *Ecology and Evolution* 4: 38. <https://doi.org/10.3389/fevo.2016.00038>.

633 Kallioniemi, Eveliina, Jens Åström, Graciela M. Rusch, Sondre Dahle, Sand-
634 dra Åström, and Jan Ove Gjershaug. 2017. “Local Resources, Linear Elements
635 and Mass-Flowering Crops Determine Bumblebee Occurrences in Moderately

- 636 Intensified Farmlands.” *Agriculture, Ecosystems & Environment* 239: 90–100.
637 <https://doi.org/https://doi.org/10.1016/j.agee.2016.12.039>.
- 638 Klein, Alexandra-Maria, Bernard E Vaissière, James H Cane, Ingolf Steffan-
639 Dewenter, Saul A Cunningham, Claire Kremen, and Teja Tscharntke. 2007.
640 “Importance of Pollinators in Changing Landscapes for World Crops.” *Pro-*
641 *ceedings of the Royal Society B: Biological Sciences* 274 (1608): 303–13. <https://doi.org/10.1098/rspb.2006.3721>.
- 643 Le Féon, Violette, Françoise Burel, Rémy Chifflet, Mickaël Henry, Agnès
644 Ricroch, Bernard E. Vaissière, and Jacques Baudry. 2013. “Solitary Bee Abun-
645 dance and Species Richness in Dynamic Agricultural Landscapes.” *Agricul-*
646 *ture, Ecosystems and Environment* 166: 94–101. <https://doi.org/https://doi.org/10.1016/j.agee.2011.06.020>.
- 648 Leifeld, Philip. 2013. “texreg: Conversion of Statistical Model Output in
649 R to LaTeX and HTML Tables.” *Journal of Statistical Software* 55 (8): 1–24.
650 <http://www.jstatsoft.org/v55/i08/>.
- 651 Linsley, E. Gorton. 1958. “The Ecology of Solitary Bees.” *Hilgardia* 27
652 (19): 543–99. <https://doi.org/10.3733/hilg.v27n19p543>.
- 653 Lonsdorf, Eric, Claire Kremen, Taylor Ricketts, Rachael Winfree, Neal
654 Williams, and Sarah Greenleaf. 2009. “Modelling pollination services across
655 agricultural landscapes.” *Annals of Botany* 103 (9): 1589–1600. <https://doi.org/10.1093/aob/mcp069>.
- 657 Lüdecke, Daniel. 2018. “Ggeffects: Tidy Data Frames of Marginal Effects
658 from Regression Models.” *Journal of Open Source Software* 3 (26): 772. <https://doi.org/10.21105/joss.00772>.
- 660 Lüdecke, Daniel, Dominique Makowski, Philip Waggoner, and Indrajeet
661 Patil. 2020. *Performance: Assessment of Regression Models Performance*. <https://CRAN.R-project.org/package=performance>.
- 663 MacIvor, J. Scott, and Laurence Packer. 2015. “‘Bee Hotels’ as Tools
664 for Native Pollinator Conservation: A Premature Verdict?” Edited by Fabio
665 S. Nascimento. *PLOS ONE* 10 (3): e0122126. <https://doi.org/10.1371/journal.pone.0122126>.
- 667 Mallinger, Rachel E., and Claudio Gratton. 2015. “Species Richness of
668 Wild Bees, but Not the Use of Managed Honeybees, Increases Fruit Set of
669 a Pollinator-Dependent Crop.” *Journal of Applied Ecology* 52 (2): 323–30.
670 <https://doi.org/10.1111/1365-2664.12377>.
- 671 Martins, Kyle T., Cécile H. Albert, Martin J. Lechowicz, and Andrew
672 Gonzalez. 2018. “Complementary Crops and Landscape Features Sustain Wild
673 Bee Communities.” *Ecological Applications* 28 (4): 1093–1105. <https://doi.org/10.1002/eap.1713>.
- 675 Michener, Charles. 2007. *The Bees of the World*. Baltimore: Johns Hopkins
676 University Press. <https://jhupbooks.press.jhu.edu/title/bees-world>.
- 677 Morandin, Lora A., and Claire Kremen. 2013. “Hedgerow Restoration Pro-
678 motes Pollinator Populations and Exports Native Bees to Adjacent Fields.”
679 *Ecological Applications* 23 (4): 829–39. <https://doi.org/10.1890/12-1051.1>.
- 680 1.

- 681 Odanaka, Katherine A., and Sandra M. Rehan. 2020. "Wild Bee Distribu-
682 tion Near Forested Landscapes Is Dependent on Successional State." *Forest*
683 *Ecosystems* 7 (1). <https://doi.org/10.1186/s40663-020-00241-4>.
- 684 Ollerton, Jeff, Rachael Winfree, and Sam Tarrant. 2011. "How Many Flow-
685 ering Plants Are Pollinated by Animals?" *Oikos* 120 (3): 321–26. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.
- 687 Papanikolaou, Alexandra D., Ingolf Kühn, Mark Frenzel, and Oliver Schweiger.
688 2017. "Semi-Natural Habitats Mitigate the Effects of Temperature Rise on
689 Wild Bees." *Journal of Applied Ecology* 54 (2): 527–36. <https://doi.org/10.1111/1365-2664.12763>.
- 691 Park, Mia G., E. J. Blitzer, Jason Gibbs, John E. Losey, and Bryan N.
692 Danforth. 2015. "Negative Effects of Pesticides on Wild Bee Communities
693 Can Be Buffered by Landscape Context." *Proceedings of the Royal Society B: Biological Sciences* 282 (1809): 20150299. <https://doi.org/10.1098/rspb.2015.0299>.
- 696 Pebesma, Edzer. 2018. "Simple Features for R: Standardized Support for
697 Spatial Vector Data." *The R Journal* 10 (1): 439–46. <https://doi.org/10.32614/RJ-2018-009>.
- 699 Pereira-Peixoto, Maria Helena, Gesine Pufal, Celso Feitosa Martins, and
700 Alexandra-Maria Klein. 2014. "Spillover of Trap-Nesting Bees and Wasps in
701 an Urban-rural Interface." *Journal of Insect Conservation* 18 (5): 815–26.
702 <https://doi.org/10.1007/s10841-014-9688-7>.
- 703 Potts, Joanne M., and Jane Elith. 2006. "Comparing Species Abundance
704 Models." *Ecological Modelling* 199 (2): 153–63. <https://doi.org/https://doi.org/10.1016/j.ecolmodel.2006.05.025>.
- 706 Potts, Simon G., Jacobus C. Biesmeijer, Claire Kremen, Peter Neumann,
707 Oliver Schweiger, and William E. Kunin. 2010. "Global Pollinator Declines:
708 Trends, Impacts and Drivers." *Trends in Ecology and Evolution* 25 (6): 345–53.
709 <https://doi.org/https://doi.org/10.1016/j.tree.2010.01.007>.
- 710 Potts, Simon G., Betsy Vulliamy, Amots Dafni, Gidi Ne'eman, and Pat
711 Willmer. 2003. "Linking Bees and Flowers: How Do Floral Communities Struc-
712 ture Pollinatore Communities?" *Ecology* 84 (10): 2628–42. <https://doi.org/10.1890/02-0136>.
- 714 Provost, Gaëtane Le, Isabelle Badenhauer, Cyrille Violle, Fabrice Re-
715 quier, Marie D'Ottavio, Marilyn Roncoroni, Louis Gross, and Nicolas Gross.
716 2020. "Grassland-to-Crop Conversion in Agricultural Landscapes Has Lasting
717 Impact on the Trait Diversity of Bees." *Landscape Ecology*, October. <https://doi.org/10.1007/s10980-020-01141-2>.
- 719 R Core Team. 2020. *R: A Language and Environment for Statistical Com-
720 puting*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- 722 Ricci, B., C. Lavigne, A. Alignier, S. Aviron, L. Biju-Duval, J. C. Bouvier,
723 J.-P. Choisis, et al. 2019. "Local Pesticide Use Intensity Conditions Landscape
724 Effects on Biological Pest Control." *Proceedings of the Royal Society B: Biological Sciences* 286 (1904): 20182898. <https://doi.org/10.1098/rspb.2018.2898>.
- 725
726

- 727 Ricketts, Taylor H., James Regetz, Ingolf Steffan-Dewenter, Saul A. Cunn-
728 ingham, Claire Kremen, Anne Bogdanski, Barbara Gemmill-Herren, et al.
729 2008. "Landscape Effects on Crop Pollination Services: Are There General Pat-
730 terns?" *Ecology Letters* 11 (5): 499–515. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2008.01157.x)
731 [0248.2008.01157.x](https://doi.org/10.1111/j.1461-0248.2008.01157.x).
- 732 Riedinger, Verena, Oliver Mitesser, Thomas Hovestadt, Ingolf Steffan-Dewenter,
733 and Andrea Holzschuh. 2015. "Annual Dynamics of Wild Bee Densities: At-
734 tractiveness and Productivity Effects of Oilseed Rape." *Ecology* 96 (5): 1351–
735 60. <https://doi.org/10.1890/14-1124.1>.
- 736 Rollin, Oriane, Vincent Bretagnolle, Axel Decourtye, Jean Aptel, Nadia
737 Michel, Bernard E. Vaissière, and Mickaël Henry. 2013. "Differences of Floral
738 Resource Use Between Honey Bees and Wild Bees in an Intensive Farming
739 System." *Agriculture, Ecosystems and Environment* 179: 78–86. [https://doi.](https://doi.org/https://doi.org/10.1016/j.agee.2013.07.007)
740 [org/https://doi.org/10.1016/j.agee.2013.07.007](https://doi.org/10.1016/j.agee.2013.07.007).
- 741 RStudio Team. 2019. *RStudio: Integrated Development Environment for R*.
742 Boston, MA: RStudio, Inc. <http://www.rstudio.com/>.
- 743 Rundlöf, Maj, Georg K. S. Andersson, Riccardo Bommarco, Ingemar Fries,
744 Veronica Hederström, Lina Herbertsson, Ove Jonsson, et al. 2015. "Seed Coat-
745 ing with a Neonicotinoid Insecticide Negatively Affects Wild Bees." *Nature* 521
746 (7550): 77–80. <https://doi.org/10.1038/nature14420>.
- 747 Rust, Richard W. 1993. "Cell and Nest Construction Costs in Two Cavity-
748 Nesting Bees (*Osmia lignaria propinqua* and *Osmia ribifloris biedermannii*)
749 (Hymenoptera: Megachilidae)." *Annals of the Entomological Society of Amer-*
750 *ica* 86 (3): 327–32. <https://doi.org/10.1093/aesa/86.3.327>.
- 751 Sánchez-Bayo, Francisco, and Kris A. G. Wyckhuys. 2019. "Worldwide
752 Decline of the Entomofauna: A Review of Its Drivers." *Biological Conser-*
753 *vation* 232: 8–27. [https://doi.org/https://doi.org/10.1016/j.biocon.](https://doi.org/https://doi.org/10.1016/j.biocon.2019.01.020)
754 [2019.01.020](https://doi.org/10.1016/j.biocon.2019.01.020).
- 755 Sgolastra, Fabio, Piotr Medrzycki, Laura Bortolotti, Maria Teresa Renzi,
756 Simone Tosi, Gherardo Bogo, Dariusz Teper, Claudio Porrini, Roberto Molowny-
757 Horas, and Jordi Bosch. 2017. "Synergistic Mortality Between a Neonicotinoid
758 Insecticide and an Ergosterol-Biosynthesis-Inhibiting Fungicide in Three Bee
759 Species." *Pest Management Science* 73 (6): 1236–43. [https://doi.org/10.](https://doi.org/10.1002/ps.4449)
760 [1002/ps.4449](https://doi.org/10.1002/ps.4449).
- 761 Shaw, Rosalind F., Benjamin B. Phillips, Toby Doyle, Judith K. Pell, John
762 W. Redhead, Joanna Savage, Ben A. Woodcock, James M. Bullock, and Juliet
763 L. Osborne. 2020. "Mass-Flowering Crops Have a Greater Impact Than Semi-
764 Natural Habitat on Crop Pollinators and Pollen Deposition." *Landscape Ecol-*
765 *ogy* 35 (2): 513–27. <https://doi.org/10.1007/s10980-019-00962-0>.
- 766 Steffan-Dewenter, Ingolf. 2002. "Landscape Context Affects Trap-Nesting
767 Bees, Wasps, and Their Natural Enemies." *Ecological Entomology* 27 (5): 631–
768 37. <https://doi.org/10.1046/j.1365-2311.2002.00437.x>.
- 769 Steffan-Dewenter, Ingolf, and Kathleen Leschke. 2003. "Effects of Habitat
770 Management on Vegetation and Above-Ground Nesting Bees and Wasps of
771 Orchard Meadows in Central Europe." *Biodiversity and Conservation* 12 (9):
772 1953–68. <https://doi.org/10.1023/a:1024199513365>.

- 773 Stuligross, Clara, and Neal M. Williams. 2020. "Pesticide and Resource
774 Stressors Additively Impair Wild Bee Reproduction." *Proceedings of the Royal*
775 *Society B: Biological Sciences* 287 (1935): 20201390. [https://doi.org/10.](https://doi.org/10.1098/rspb.2020.1390)
776 [1098/rspb.2020.1390](https://doi.org/10.1098/rspb.2020.1390).
- 777 Tschardtke, Teja, Jason M. Tylianakis, Tatyana A. Rand, Raphael K.
778 Didham, Lenore Fahrig, Péter Batáry, Janne Bengtsson, et al. 2012. "Land-
779 scape Moderation of Biodiversity Patterns and Processes - Eight Hypothe-
780 ses." *Biological Reviews* 87 (3): 661–85. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-185X.2011.00216.x)
781 [185X.2011.00216.x](https://doi.org/10.1111/j.1469-185X.2011.00216.x).
- 782 Vanbergen, Adam J, and the Insect Pollinators Initiative. 2013. "Threats
783 to an Ecosystem Service: Pressures on Pollinators." *Frontiers in Ecology and*
784 *the Environment* 11 (5): 251–59. <https://doi.org/10.1890/120126>.
- 785 Vicens, Narcís, and Jordi Bosch. 2000. "Weather-Dependent Pollinator Ac-
786 tivity in an Apple Orchard, with Special Reference to *Osmia cornuta* and *Apis*
787 *mellifera* (Hymenoptera: Megachilidae and Apidae)." *Environmental Entomol-*
788 *ogy* 29 (3): 413–20. <https://doi.org/10.1603/0046-225X-29.3.413>.
- 789 Woodcock, B. A., J. M. Bullock, R. F. Shore, M. S. Heard, M. G. Pereira,
790 J. Redhead, L. Ridding, et al. 2017. "Country-Specific Effects of Neonicotinoid
791 Pesticides on Honey Bees and Wild Bees." *Science* 356 (6345): 1393–5. <https://doi.org/10.1126/science.aaa1190>.
- 792
793 Woodcock, Ben A., Nicholas J. B. Isaac, James M. Bullock, David B. Roy,
794 David G. Garthwaite, Andrew Crowe, and Richard F. Pywell. 2016. "Impacts
795 of Neonicotinoid Use on Long-Term Population Changes in Wild Bees in Eng-
796 land." *Nature Communications* 7 (1). <https://doi.org/10.1038/ncomms12459>.
- 797 Zurbuchen, Antonia, Lisa Landert, Jeannine Klaiber, Andreas Müller, Silke
798 Hein, and Silvia Dorn. 2010. "Maximum Foraging Ranges in Solitary Bees:
799 Only Few Individuals Have the Capability to Cover Long Foraging Distances."
800 *Biological Conservation* 143 (3): 669–76. [https://doi.org/https://doi.org/](https://doi.org/https://doi.org/10.1016/j.biocon.2009.12.003)
801 [10.1016/j.biocon.2009.12.003](https://doi.org/https://doi.org/10.1016/j.biocon.2009.12.003).

802 **Appendix A : variables included in full models****Table 2** Variables included in full models.

Type	Name	Source
<i>Local</i>	Farming system (in field crop model)	FBO
	Type of meadow (in meadow model)	
	Young hedgerow	
	Old hedgerow	
	Grassy strip	
	Road	
	Woody margin	
Ditch		
<i>Landscape</i>	Rapeseed cover (current and previous year)	RPG
	Sunflower cover (current and previous year)	
	Temporary meadow cover (current and previous year)	
	Permanent meadow cover (current and previous year)	CLC
	Orchard cover (current and previous year)	
	Perimeter of forests	
<i>Interactions</i>	Rapeseed cover x Farming system	
	Sunflower cover x Farming system	
	Permanent meadow cover x Farming system	
<i>Control</i>	Temperature	E-OBS
	Precipitation	
	Number of days until the observation date	FBO

Submitted Version

803 **Appendix B : variance inflation factors****Table 3** Variance inflation factors for solitary bee models, obtained with the *performance* package (Lüdecke, Makowski, Waggoner, & Patil, 2020).

	VIF - Zero model		VIF - Count model	
	Field crops	Meadows	Field crops	Meadows
Landscape variables				
Area of rapeseed (current year)	1.1613843	1.4331223	1.1760177	1.1637416
Area of rapeseed (previous year)	1.2575812	1.3411484	1.490103	1.1544491
Area of sunflower (current year)	1.1507636	1.2390304	1.1240526	2.7817675
Area of sunflower (previous year)	1.312954	1.1613843	1.3028097	3.0061777
Area of permanent meadows	1.1793103	1.1507636	1.175312	1.4221678
Area of temporary meadows (current year)		1.312954		2.3629475
Area of temporary meadows (previous year)		1.3230414		1.9896526
Local variables				
Organic farming	1.3230414		3.0345493	
Permanent meadow		1.2575812		1.1882082
Perimeter of forests	1.0325193			
Road	1.0603447			1.0680997
Young hedgerow		1.1793103		
Old hedgerow	1.058275	1.0325193	1.0470096	
Interactions				
Area of rapeseed (cur. year):Organic farming	5.0463066		2.821749	
Area of rapeseed (prev. year):Organic farming	5.0463066		1.5065585	
Area of sunflower (cur. year):Organic farming	5.0463066		1.4331223	
Area of sunflower (prev. year):Organic farming	5.0463066		1.3411484	
Area of permanent meadows:Organic farming	5.0463066		1.2390304	
Control variables				
Temperature	1.3516973	1.058275	1.4147727	1.3678506
Precipitation	1.2405514	1.0603447	1.2433694	1.3891674
Number of days	1.1778804	1.3516973	1.2125183	1.1144494

804 Appendix C : residual diagnostics

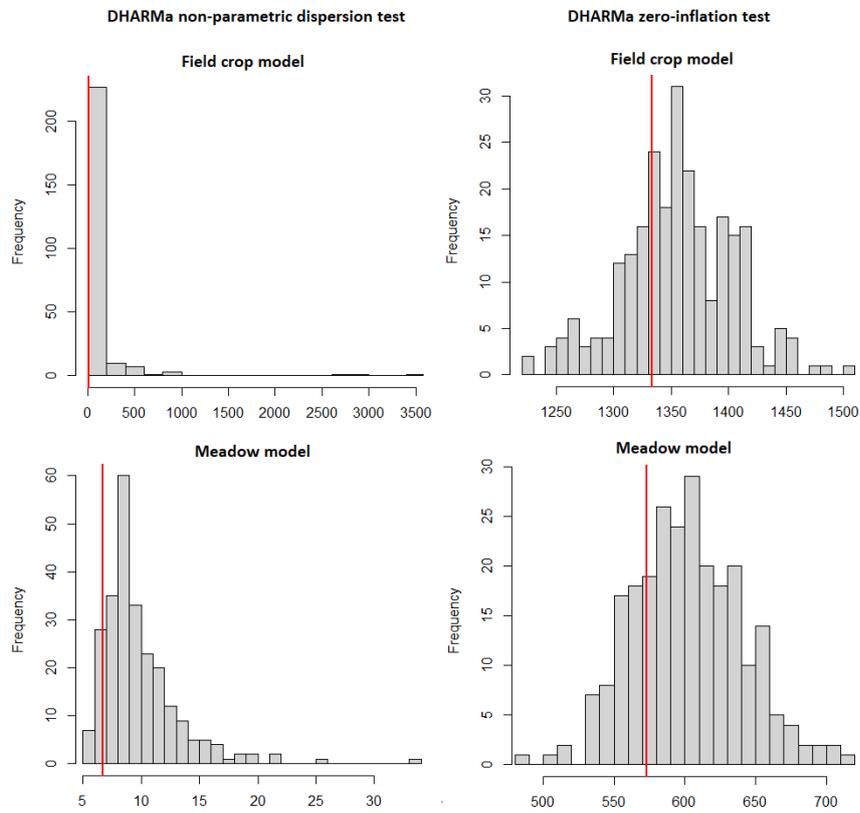


Fig. 6 Residual diagnostics for solitary bee models, obtained with the *DHARMA* package (Hartig, 2020). Grey bars are simulated values, the red line is the fitted model.

805 Appendix D : Durbin-Watson tests

806 To detect the presence of temporal autocorrelation in the residuals, we applied the Durbin
 807 Watson test to the sites that were monitored at least three times in the year. Thus, we
 808 could test 393 site/year couples in our field crop edge model and 174 site/year couples in
 809 our meadow edge model.

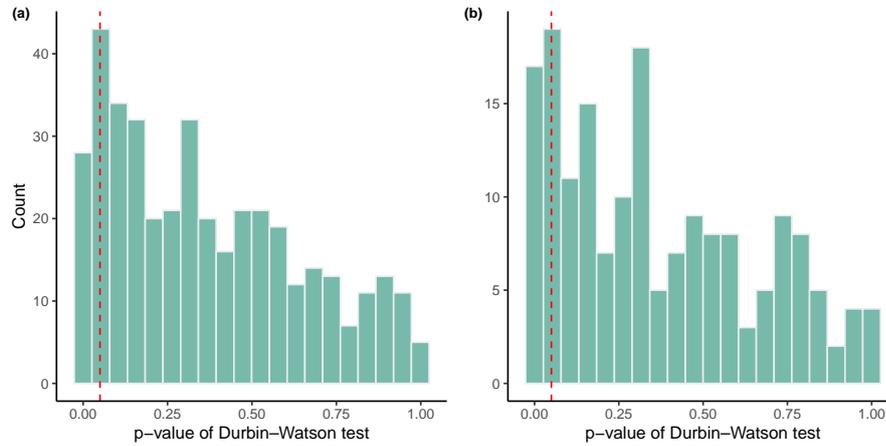


Fig. 7 Distribution of Durbin-Watson test p-values, for residuals of (a) field crop edge model or (b) meadow edge model. Red dashed line is the 0.05 threshold.

810 In our field crop edge model, a total of 51 site/year couples (13%) have a p-value
 811 than 0.05. In our meadow edge model, a total of 27 site/year couples (15.5%) have a p-value
 812 lower than 0.05.

813 Appendix E : alternative models

Table 4 Comparison of hurdle model outputs examining the relationship between the presence of tubes ("Zero model") or their abundance conditional on presence ("Count model") and environmental variables, for trap nests set up in **field crop edges**. The table shows the parameter estimates, with standard errors in parentheses. Parameters with a p-value < 0.05 are reported in bold. All variables were standardized and centered.

	Current model		Alternative models	
	All counts of mud-sealed tubes	Highest count of mud-sealed tubes	All counts of all tubes	
Count model				
Intercept (conventional farming, no landscape elements nearby)	1.32 (0.14)***	1.93 (0.19)***	1.73 (0.10)***	
Area of rapeseed (current year)	0.04 (0.06)	-0.12 (0.10)	-0.03 (0.04)	
Area of rapeseed (previous year)	0.31 (0.09)***	0.25 (0.12)*	0.31 (0.06)***	
Area of sunflower (current year)	0.03 (0.07)	-0.12 (0.10)	0.01 (0.04)	
Area of sunflower (previous year)	-0.04 (0.09)	0.19 (0.13)	-0.01 (0.06)	
Area of permanent meadows	0.27 (0.09)**	0.34 (0.10)***	0.25 (0.07)***	
Organic farming	-0.75 (0.43)	-1.58 (0.56)**	-0.63 (0.29)*	
<i>Old hedgerow</i>	-0.14 (0.18)	-0.13 (0.19)	-0.12 (0.13)	
Area of rapeseed (cur. year):Organic farming	-1.51 (0.70)*	-2.19 (1.14)	-1.04 (0.48)*	
Area of rapeseed (prev. year):Organic farming	-0.31 (0.31)	-0.60 (0.39)	-0.20 (0.24)	
Area of sunflower (cur. year):Organic farming	1.03 (0.46)*	-0.21 (0.69)	-0.03 (0.11)	
Area of sunflower (prev. year):Organic farming	0.19 (0.28)	0.13 (0.30)	0.10 (0.17)	
Area of permanent meadows:Organic farming	-0.07 (0.28)	-0.19 (0.33)	-0.15 (0.21)	
Temperature	0.40 (0.07)***	0.08 (0.11)	0.36 (0.05)***	
Precipitation	0.37 (0.05)***	0.20 (0.11)	0.24 (0.04)***	
<i>Number of days</i>	0.02 (0.04)	-0.07 (0.11)	0.23 (0.03)***	
Zero model				
Intercept (conventional farming, no landscape elements nearby)	-0.90 (0.30)**	1.01 (0.30)***	0.38 (0.24)	
Area of rapeseed (current year)	-0.14 (0.11)	-0.03 (0.15)	-0.01 (0.11)	
Area of rapeseed (previous year)	0.50 (0.15)***	0.31 (0.17)	0.07 (0.13)	
Area of sunflower (current year)	-0.07 (0.12)	0.04 (0.14)	0.29 (0.12)*	
Area of sunflower (previous year)	-0.41 (0.17)*	-0.37 (0.18)*	-0.26 (0.15)	
Area of permanent meadows	0.69 (0.19)***	0.51 (0.16)**	0.43 (0.16)**	
<i>Perimeter of forests</i>	0.37 (0.19)*	-0.02 (0.15)	0.47 (0.15)**	
Organic farming	0.48 (0.57)	0.27 (0.64)	-0.06 (0.44)	
<i>Road</i>	-0.68 (0.31)*	-0.71 (0.31)*	-0.97 (0.27)***	
<i>Old hedgerow</i>	0.59 (0.31)	0.48 (0.29)	0.93 (0.27)***	
Area of rapeseed (cur. year):Organic farming	-0.33 (0.82)	0.22 (1.01)	-0.83 (0.68)	
Area of rapeseed (prev. year):Organic farming	0.72 (0.70)	1.47 (0.96)	0.64 (0.56)	
Area of sunflower (cur. year):Organic farming	-0.27 (0.41)	-0.80 (0.76)	-0.52 (0.30)	
Area of sunflower (prev. year):Organic farming	-0.79 (0.52)	-0.03 (0.63)	-0.44 (0.42)	
Area of permanent meadows:Organic farming	-0.30 (0.59)	-0.12 (0.77)	-0.16 (0.48)	
Temperature	1.32 (0.14)***	1.40 (0.20)***	0.95 (0.12)***	
Precipitation	0.66 (0.11)***	0.29 (0.19)	0.55 (0.10)***	
<i>Number of days</i>	0.60 (0.09)***	2.42 (0.29)***	1.29 (0.10)***	

***p < 0.001, **p < 0.01, *p < 0.05

Table 5 Comparison of hurdle model outputs examining the relationship between the presence of tubes ("Zero model") or their abundance conditional on presence ("Count model") and environmental variables, for trap nests set up in **meadows edges**. The table shows the parameter estimates, with standard errors in parentheses. Parameters with a p-value < 0.05 are reported in bold. All variables were standardized and centered.

	Current model	Alternative models	
	All counts of mud-sealed tubes	Highest count of mud-sealed tubes	All counts of all tubes
Count model			
Intercept (temporary meadow, no landscape elements nearby)	1.63 (0.20)***	1.93 (0.29)***	1.91 (0.18)***
Area of rapeseed (current year)	-0.04 (0.06)	-0.15 (0.13)	0.03 (0.06)
Area of rapeseed (previous year)	0.24 (0.09)**	0.27 (0.12)*	0.16 (0.08)*
Area of sunflower (current year)	0.10 (0.16)	0.19 (0.27)	0.17 (0.09)*
Area of sunflower (previous year)	-0.10 (0.16)	-0.16 (0.22)	-0.15 (0.10)
Area of permanent meadows	0.11 (0.11)	0.12 (0.13)	0.10 (0.10)
Area of temporary meadows (current year)	-0.40 (0.16)*	-0.35 (0.20)	-0.25 (0.14)
Area of temporary meadows (previous year)	0.30 (0.15)*	0.33 (0.18)	0.12 (0.14)
Permanent meadow	-0.01 (0.18)	0.18 (0.25)	-0.06 (0.16)
Road	-0.50 (0.20)*	-0.37 (0.25)	-0.51 (0.19)**
Temperature	0.24 (0.10)*	0.29 (0.17)	0.12 (0.09)
Precipitation	0.25 (0.09)**	0.22 (0.16)	0.26 (0.08)**
Number of days	0.18 (0.06)**	0.16 (0.18)	0.24 (0.05)***
Zero model			
Intercept (temporary meadow, no landscape elements nearby)	-1.72 (0.59)**	0.86 (0.40)*	-0.24 (0.45)
Area of rapeseed (current year)	0.31 (0.20)	0.19 (0.30)	0.18 (0.17)
Area of rapeseed (previous year)	0.13 (0.29)	0.06 (0.25)	0.04 (0.24)
Area of sunflower (current year)	-0.35 (0.30)	-0.32 (0.35)	0.02 (0.21)
Area of sunflower (previous year)	-0.16 (0.38)	-0.15 (0.30)	-0.33 (0.29)
Area of permanent meadows	1.03 (0.38)**	0.64 (0.25)*	0.75 (0.29)**
Area of temporary meadows (current year)	1.15 (0.46)*	0.37 (0.32)	0.50 (0.38)
Area of temporary meadows (previous year)	-1.09 (0.49)*	-0.22 (0.32)	-0.56 (0.40)
Permanent meadow	0.51 (0.40)	-0.31 (0.42)	0.48 (0.36)
Young hedgerow	1.16 (0.66)	0.08 (0.59)	0.43 (0.53)
Old hedgerow	0.41 (0.62)	0.48 (0.42)	0.59 (0.49)
Temperature	1.79 (0.29)***	0.97 (0.28)***	1.81 (0.27)***
Precipitation	1.44 (0.26)***	0.04 (0.28)	1.10 (0.23)***
Number of days	1.07 (0.16)***	2.10 (0.35)***	1.38 (0.16)***

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$