Temperate agroforestry systems provide greater pollination service than monoculture

Article

Accepted Version

It is advisable to refer to the publisher's version if you intend to cite from the work. See Guidance on citing.

To link to this article DOI: http://dx.doi.org/10.1016/j.agee.2020.107031

Publisher: Elsevier

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

1 **Temperate agroforestry systems provide greater pollination service than**

2 **monoculture**

3 Alexa Varah[a,1] *, Hannah Jones[a], Jo Smith[b] and Simon G Potts[a]

4 [a] Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, Reading

5 RG6 6AR, United Kingdom

6 [b] The Organic Research Centre, Elm Farm, Hamstead Marshall, Newbury, Berkshire RG20 0HR, United Kingdom.

7 * Corresponding author: a.varah@nhm.ac.uk

---

[1] Present address: Natural History Museum, Cromwell Road, London SW7 5BD United Kingdom
Email: a.varah@nhm.ac.uk

8 **Abstract**

9 Insect pollination is a globally important ecosystem service, contributing to crop yields, production

10 stability and the maintenance of wild plant populations. Ironically, agriculture is one of the major

11 global drivers of wild insect pollinator decline. At the same time, increasing human population is

12 driving ever greater demands on crop production. Agroforestry (AF) – a more diverse farming

13 system integrating woody and agricultural crops – can theoretically reconcile high production with

14 provision of ecosystem services such as pollination. However, empirical studies of pollination in

15 temperate AF systems are almost entirely lacking. We sought to fill this knowledge gap by assessing

16 whether AF can provide increased pollination service compared to monoculture (MC) systems. Six

17 UK sites, each containing an AF and a MC system, were studied over three years. Wild pollinator

18 abundance and diversity were used as proxies for the magnitude and stability, respectively, of the

19 pollinating community. We also directly measured pollination service as seed set in a wild plant

20 phytometer. We found that temperate AF systems can provide greater pollination service than MC:

21 AF treatments had twice as many solitary bees and hoverflies, and in arable systems 2.4 times more

22 bumblebees, than MC treatments. AF also had 4.5 times more seed set compared to MC in one of

23 the two years. At 40% of site-by-year sampling units, species richness of solitary bees was on

24 average 10.5 times higher in AF treatments. This provides evidence in favour of the expectation

25 that AF systems can support higher pollinator richness, and therefore greater potential stability, of

26 pollination service. For the other sampling units, and for bumblebees (*Bombus* spp.), there was no

27 treatment effect on species richness. Further work is needed to investigate the effect of AF on

28 species richness and its mechanistic basis. Our results also highlight the importance of AF system

29 design, ensuring that ecosystem services outcomes are explicitly planned at the design stage. We

30 suggest that AF has a role to play in improving the sustainability of modern farming and in

31 mitigating the ongoing loss of wild pollinating insects, which is strongly driven by prevailing

32 agricultural practices.

33 **Keywords:** Agroforestry, pollination service, bumblebee, hoverfly, solitary bee, abundance, richness

1. Introduction

Intensive agriculture is one of the primary causes of biodiversity loss globally (Foley et al., 2005; IPBES, 2019; Newbold et al., 2015); ironically, it is also heavily reliant on biodiversity to support the ecosystem functions and services that underpin food production (Dainese et al., 2019; Garibaldi et al., 2013). Of these, pollination service has received particular attention as 35% of global crop production volume is dependent on insect pollination to some extent (Klein et al., 2007), and pollinators affect both the quantity (Castle et al., 2019; Fijen et al., 2018) and quality (Garratt et al., 2014; Klatt et al., 2013) of food produced. Despite widespread awareness of their importance, wild pollinating insect abundance and diversity continue to decline in some regions of the world (Potts et al., 2016, 2010; Powney et al., 2019). These pollinator declines, as for wider biodiversity, are driven in large part by agricultural intensification (Goulson et al., 2015; Grab et al., 2019). There is consensus that agriculture-related factors (habitat loss, and pollutants such as synthetic pesticides and fertilisers) are amongst the major drivers of insect declines worldwide (Sánchez-Bayo and Wyckhuys, 2019; Vanbergen and the IPI, 2013). These reductions in pollinator abundance and diversity are thought to have negative effects on global food production and wild plant pollination (Grab et al., 2019; Potts et al., 2016): global trends are already showing lower mean relative yields and lower yield growth in crops with greater pollination dependence (Deguines et al., 2014; Garibaldi et al., 2011a).

Efforts to mitigate loss of biodiversity in farmed land focus largely on increasing wild plant diversity as it is known that this can benefit wild pollinating insects (Isbell et al., 2017; Kovács-Hostyánszki et al., 2017). In Europe, practical interventions to increase floral resources and plant structural diversity on farmland have predominantly been encouraged through agri-environment schemes introduced via the Common Agricultural Policy. These have had some positive effects on wild bees (Scheper et al., 2013) but have less success at increasing biodiversity in field centres (Batáry et al., 2015) and, overall, numbers of insect pollinators continue to decline in many areas of the world (Goulson et al., 2015; Potts et al., 2016; Powney et al., 2019).

60   The trade-off with biodiversity loss has been high yields; however, it is becoming evident that the

61   yield benefits of intensive agriculture are beginning to plateau and, in some countries, are even

62   falling (Lin and Huybers, 2012; Ray et al., 2012). At the same time, global population and thus food

63   demand are increasing. These facts, combined with the continuing degradation of agroecosystems

64   and the realisation that farmed land is no longer providing the ecosystem services it once did, have

65   led to calls for more environmentally sustainable, yet still intensive, farming practices (Garibaldi et

66   al., 2016; Isbell et al., 2017; Pretty et al., 2018). These recognise the key role that biodiversity plays

67   in food production (Dainese et al., 2019; IPBES, 2019; Rockström et al., 2017). Research is needed

68   to ascertain the implications for pollinators of these alternative farming practices (Dicks et al.,

69   2013).

70   AF is one such practice, integrating woody species with crop or livestock species. In modern AF

71   systems, crops/livestock are grown in alleys between tree rows which can produce timber, fruit,

72   nuts or any other woody product (Smith et al., 2012). It thus has inherently greater plant diversity

73   per unit area (in terms of both crops and wild plants, such as those in the tree row understorey).

74   Furthermore, this increased plant diversity extends throughout the field rather than being confined

75   to field margins. Thus, in intensively-farmed landscapes, AF systems could benefit biodiversity by

76   increasing the permeability of the agricultural matrix (Vandermeer and Perfecto, 2007). Indeed,

77   improving habitat in the cropped area has been shown to be of greater relative importance in

78   mitigating biodiversity loss than improving habitat in field margins (Butler et al., 2009). AF systems

79   also increase edge density in agroecosystems, which has been shown to increase insect pollinator

80   abundance and promote ecosystem service provision (Martin et al., 2019).

81   The interactions created in AF systems, when carefully managed, are theorised to provide

82   numerous benefits (Jose, 2009; Kay et al., 2018; Kuyah et al., 2017) for example through improved

83   provision of nesting, shelter and foraging resources (Kay et al., 2019; Nicholls and Altieri, 2013;

84   Persson et al., 2015). Foraging resources, in particular, directly regulate bee populations (Roulston

85   and Goodell, 2011), and bee populations also respond positively to linear elements (Kallioniemi et

4

86   al., 2017). Despite its proposed benefits, AF remains understudied in temperate systems and

87   implementation has been low; due, in part, to lack of data demonstrating the economic and

88   environmental outcomes of these systems (Meyer, 2012; Rhodes et al., 2018; Valdivia et al., 2012).

89   In the tropics, there is evidence of improved pollinator abundance and diversity in AF systems

90   (Briggs et al., 2013; Hass et al., 2018; Hoehn et al., 2012) but applied work on pollination in

91   temperate AF systems is almost non-existent: before this study (for preliminary results see Varah et

92   al. (2013)) there was just one case study which found increased abundance of airborne arthropods

93   in an AF system (Peng et al., 1993).

94   To help fill this knowledge gap, we aimed to assess whether AF can benefit wild pollinators. To do

95   this we compared wild insect pollinator abundance, species richness, and pollination service in six

96   paired organic AF and MC systems in the United Kingdom (UK). We focused on wild insect

97   pollinators (we chose bumblebees (*Bombus* spp.), solitary bees, and hoverflies (Syrphidae)) because

98   (a) the majority of pollination service is provided by wild, rather than managed, pollinating species

99   (Breeze et al., 2011; Garibaldi et al., 2013; Smith et al., 2011), and (b) although honey bees are

100   important crop pollinators, their abundance is primarily driven by beekeeper decision-making

101   rather than environmental factors. We assumed that a greater abundance and/or greater diversity

102   of pollinating insects results in improved pollination service; either in terms of the magnitude of the

103   service, which has been linked more closely to pollinator abundance (Castle et al., 2019; Garibaldi

104   et al., 2013; Winfree et al., 2015; Woodcock et al., 2019), or the stability of the service, linked more

105   closely to pollinator diversity (Garibaldi et al., 2011b; Hoehn et al., 2008; Winfree et al., 2018).

106   We predicted:

107   (1) Higher pollinator abundance in AF than MC.

108   (2) Higher pollinator species richness in AF than MC.

109   (3) Higher pollination service in AF than MC.

2. Methods

2.1 Study sites and experimental design

The effect of AF systems on pollination service was assessed in the UK using paired fields, one of which had an agricultural crop plus a tree crop (the AF treatment), the other of which had only the agricultural crop (the MC treatment). In this way we set up six sites, each with an AF system paired with an 'equivalent' agricultural MC. No suitable forestry MC (or other woody species MCs) were available, so comparison of AF *vs* tree MC systems was not possible. Sites were chosen based on several biological and logistical considerations (Appendix A). The sites encompassed a range of landscape contexts, regions and AF types (Table A.1), allowing broad conclusions to be drawn about UK AF systems. Both arable AF (silvoarable) and pasture AF (silvopasture) sites were included. A summary of fieldwork carried out at each site is given in Appendix A, Table A.2.

Paired fields were located on the same farm in order to control for landscape and site-specific effects. They were matched as closely as possible in terms of soil type, slope, aspect and previous management. The only exception was at the Suffolk site (WAF) in 2011 where a suitable MC field was not available on site, so a paired field was chosen on a farm 8 km away. This pair was only used for some of the analyses (details below). Agricultural crop type and management were as similar as possible within each pair. Such field-scale comparisons have been shown to be a reliable way of determining effects of agri-environment management options (Kleijn and van Langevelde, 2006). All sites were managed organically (no conventionally-managed sites were available). Organic farming can support higher pollinator abundance and diversity, especially at the field scale (Gabriel et al., 2013; Lichtenberg et al., 2017), although with mixed results in grassland (Scheper et al., 2013). The implication for this study is that the observed abundance and/or diversity of pollinators is likely to be higher than had non-organic fields been used, at least in arable fields. However, as both treatments were organic, the comparison remains valid and any treatment effect should also apply to conventional systems; and perhaps to an even greater degree, as larger effect sizes have been observed with increased local contrast in floral resources (Scheper et al., 2015).

136 In the event of unplanned differences in the cutting regime across paired fields at pasture sites,

137 pollinator data from the affected sampling occasion(s) were excluded from analyses (Tables A.3 and

138 A.4), because differences in cutting regime and sward structure have been shown to have a major

139 short-term effect on pollinator abundance and diversity (Buri et al., 2014; Potts et al., 2009). All

140 data from the Suffolk site (WAF) in 2011 were excluded from bumblebee and hoverfly analyses

141 (although retained in solitary bee analyses) because the sown ley mixtures in the paired fields

142 differed greatly in clover abundance (it was greater in the MC treatment; further details and

143 justifications in Appendix A). The potential impacts of these decisions were assessed in separate

144 analyses, which gave consistent results (Appendix B, Tables B.4-B.6 & B.10) although with slightly

145 weaker data-based model selection, indicating the decisions were justified.

146 *2.2 Estimating pollination service*

147 We monitored bumblebees, solitary bees and hoverflies as these are known to be the main insect

148 pollinating taxa in the UK; butterflies contribute relatively little to crop pollination in northern

149 Europe (Jennersten, 1984). Abundance (Section 2.2.1) and species richness (Section 2.2.2) of

150 pollinators were used as proxies for pollination service (see Introduction for literature supporting

151 the assumptions made here) as both have been directly linked to plant reproductive success and

152 pollination service provision (Dainese et al., 2019; Winfree et al., 2018, 2015). Pollinator abundance

153 was estimated using timed transect walks and species richness using pan traps (O'Connor et al.,

154 2019). Pollination service was also measured directly using phytometer plants (Section 2.2.3).

155 *2.2.1 Abundance*

156 Abundance within each taxon was measured as total numbers of individuals per field recorded

157 during a field season. Standardised transect walks were used to assess numbers of individuals.

158 Transect walks give a good indication of habitat associations as they are area-based rather than

159 activity-based. At each site a 200m-long transect was set up in each treatment in the spring of

160 2011. Unambiguously identifiable individuals seen within 2.5m on each side of the line and 2.5m in

161 front of the observer were recorded. Because many pollinator species are hard to identify outside a

162 laboratory setting, unidentifiable pollinator specimens were netted and killed quickly with ethyl

163 acetate for laboratory identification. Transects were set up at least 25m from the end of the AF

164 alley, or from the field boundary in the MC, to avoid edge effects. In AF systems, half of each

165 transect (100m) was situated in the centre of the alley and the other half ran along the edge of the

166 alley in order to sample both environments. Transects were walked at a rate of 5m min^{-1} between

167 10:45h and 15:45h, and only when weather conformed to UK Butterfly Monitoring Scheme

168 standards (http://www.ukbms.org/Methods.aspx) as insect pollinators forage in these conditions.

169 Weather conditions were monitored throughout the transect using a Kestrel 3500 hand-held

170 weather meter. Transects were carried out from the end of March until the end of September in

171 2011 and from April-September in 2012 to encompass peak flower blooming and pollinator flight

172 periods. At one site (WAF, site details in Appendix A) an additional survey round was undertaken in

173 March 2013 to capture the flowering period of the tree species at that site.

174 One transect was walked in each treatment (AF or MC) per visit. Sites were visited between four

175 and six times during the season (number of successful visits depended on the weather and the farm

176 management). At most sites, five visits were achieved in 2011 and four in 2012. Visits were at least

177 a month apart to avoid re-sampling the same individuals on each visit. Although different sites were

178 not sampled with equal intensity, each pair of fields within a site was sampled equally. Site was

179 included in models as a random effect, allowing direct comparisons of abundance to be made.

180 *2.2.2 Species richness*

181 Species richness was chosen as a suitable diversity measure because (a) it is often used in studies

182 looking at the effects of agri-environmental management or habitat quality on pollinators (e.g.

183 Kleijn and van Langevelde 2006, Concepción *et al.* 2012); (b) it is suitable for all spatial scales; and

184 (c) it is an easily-understood index of community structure (Gotelli and Colwell, 2011). EstimateS

185 was used for species richness calculations (Colwell, 2013). Sites were not all sampled an equal

186 number of times, so rarefaction (bumblebees) and extrapolation (solitary bees) were used in order

187 to allow analysis of species richness across all sites (Gotelli and Colwell, 2001; Colwell *et al.*, 2012).

188 Bumblebee data was rarefied to the lowest number of sampling occasions at any site (*n*=4) as

189 numbers caught were not high enough to allow reliable extrapolation. Solitary bee numbers were

190 higher so species richness could reliably be extrapolated to the highest number of sampling

191 occasions at any site (*n*=14) (an analysis of rarefied solitary bee data gave consistent results, Table

192 B.9, Figure B.1). Workers of *Bombus terrestris* and *B. lucorum* (buff-tailed and white-tailed

193 bumblebees) are difficult to tell apart so these two species were recorded as one aggregate species.

194 All solitary bees were identified to species by Ellen Moss (University of Reading). Hoverfly species

195 richness was not investigated.

196 Pan traps have been shown to be the best single method for assessing bee SR (Westphal *et al.*,

197 2008; Nielsen *et al.*, 2011). UV-bright pan traps were set up on each visit and left out from 08:00h-

198 17:00h. Three colours (one yellow, one blue and one white pan) were used at each sampling

199 location as different pollinator groups may be attracted to different colours (Campbell and Hanula,

200 2007). Sampling locations were positioned in a diagonal line across an AF alley. Six sampling

201 locations were used per treatment in 2011, and twelve sampling locations were used per treatment

202 in 2012 (six sampling locations in each of 2 alleys). This pattern and orientation were mimicked in

203 the MC control fields. Pan trap sampling was carried out on the same sampling occasions as

204 transect walks.

205 At arable sites pan traps were positioned on stands at crop height. At pasture sites pans were

206 placed on the ground on a square of black mulch fabric to ensure the same background colour at

207 each position. Insects collected from each pan were bagged and taken back to the laboratory where

208 they were frozen until identification.

209 *2.2.3 Seed production*

210 In 2012 and 2013, phytometers (potted plants) were used to estimate pollination service directly at

211 a subset of sites (Table A.2) as they are a reliable method for measuring pollination service

212 (Woodcock et al., 2014). The plants chosen were California poppy (*Eschscholtzia californica*) as they

213 are self-incompatible, pollinated by generalist species, do not occur in the landscape (therefore all

214 pollen comes from the phytometers), and the seeds are easy to count. The phytometers used in

215 this study performed well in field trials and plants from the same batch were used successfully in

216 other studies (Hardman et al., 2016). Hardman et. al. (2016) give further justifications for choosing

217 California poppy.

218 Prior to exposure, five developing buds were tagged and all other buds removed. Plants were then

219 placed in the field: on the ground in pasture systems and on upturned buckets in arable systems to

220 ensure the flowers were level with the top of the crop. Phytometers were protected with chicken

221 wire cages and 10 organic slug pellets per pot. They were watered as necessary.

222 Phytometers were exposed for two weeks in July and August, and additional flowers were tagged

223 as they opened (up to 20 additional flowers in 2012, and 30 in 2013). Phytometers were then

224 placed in pollinator exclusion cages while tagged fruits ripened (any subsequent developing buds

225 were removed daily, and plants were watered as necessary). Seed set was assessed by counting the

226 number of fully-developed seeds per fruit.

227 Phytometer positioning in the field followed the same pattern as the pan trap positions, but

228 phytometer plants were positioned 5m further down the alley so that they were not in the same

229 place as the pan traps. In 2012, two arable and one pasture site were used and one phytometer

230 plant was placed at each position. In 2013 the phytometer experiment was beset with issues. First,

231 land use could not be kept the same as in 2012 because one of the arable sites changed the crop

232 from arable to ley and although another arable site was set up with phytometers in 2013, work

233 there had to be abandoned due to a severe weed problem. Thus, in 2013 three pasture sites were

234 used. Furthermore, in 2013 two plants were used per position at two of the three pasture sites but,

235 due to unforeseen circumstances, only one plant was used per position at the third pasture site and

236 at the (subsequently abandoned) arable site. Finally, due to an error, phytometer plants at two of

237   the three sites (SD & WAF) in 2013 were closer to each other in MC treatments than in AF

238   treatments. In the third site (LHF) distances were equal. The implications of these issues are

239   discussed later. For transparency, we include an analysis of the 2013 phytometer data and attempt

240   to account for these discrepancies; however, the results merely serve to highlight the problems

241   inherent in the dataset. Partly because of these discrepancies, phytometer data were analysed

242   separately for 2012 and 2013.

243   *2.3 Estimation of other variables expected to influence abundance or species richness*

244   Because it was not possible to control for effects other than treatment, several other possible

245   predictors of pollinator and plant species richness and abundance were measured, based on the

246   literature (Table A.5). These were: the species richness of insect-pollinated plants in field

247   boundaries (both hedges and margins, method in Appendix A); the area covered by the field

248   boundaries (measured from farm maps and Google Earth); the distance to the nearest field

249   boundary from the data collection area (measured on the ground); the number of hedged field

250   boundaries; the type of land use (arable or pasture); the percentage of the transect that was sunny

251   (time estimated during transect); and the percentage of semi-natural habitat (SNH) in the

252   surrounding landscape. %SNH in a 1km buffer around field perimeters was calculated from Priority

253   Habitat Inventory for South East England using ArcMap 10 GIS software. This buffer size

254   encompasses the predominant flight ranges of wild bees (Greenleaf et al., 2007; Zurbuchen et al.,

255   2010). Further methodological details given in Appendix A.

256   Finally, because the effect of treatment on pollinator species richness and abundance may be

257   mediated through treatment effects on plant species richness (Borer et al., 2012; Scherber et al.,

258   2010), we estimated the plant species richness of the cropped area (method in Appendix A) and

259   tested for correlations with pollinator abundance or species richness. In AF systems, the cropped

260   area included the tree rows.

261 *2.4 Statistical analyses*

262 An information theoretic (IT) approach was adopted, using model averaging to allow inferences to

263 be drawn from weighted support over several models (multi-model inference). Standard IT practice

264 is to first generate a highly-parameterised global model with all the biologically relevant

265 parameters (Burnham and Anderson, 2002; Grueber et al., 2011; Harrison et al., 2018). The global

266 model (which is not used for inference) is used to generate all possible lower-dimensional sub-

267 models (in effect, all possible hypotheses). These more parsimonious lower-dimensional models are

268 then compared against each other to find out their relative worth. The ones with the highest

269 relative worth are used for inference. Statistical analyses were carried out in R (R Development

270 Core Team, 2019).

271 An extensive literature search was carried out to identify possible predictor variables for inclusion

272 in global models (Table A.5) (Burnham et al., 2011; Elliott and Brook, 2007). The final choice of

273 predictor variables and interactions included in global models was based on evidence from the

274 literature and on basic data exploration. Variables that did not appear to be having a strong effect

275 when investigated graphically were nonetheless included in global models if there was a scientific

276 reason to suspect they might have some effect.

277 Global models (Table A.6) were all initially built as generalised linear mixed effects models

278 (GLMMs), fitted by maximum likelihood. Model fit was based on the global model only (Burnham et

279 al., 2011; Harrison et al., 2018; Symonds and Moussalli, 2011). To allow comparison of the relative

280 strength of parameter estimates after model averaging, continuous independent variables were

281 standardised prior to model building using the *arm* package (Gelman et al., 2013) or, for negative

282 binomial models, the *rescale* function in R. For species richness and phytometer 2012 data, error

283 structures were Poisson or Gaussian (*glmer* and *lmer* functions respectively, package *lme4* (Bates et

284 al., 2015)). To reduce overdispersion, error structures for abundance models were Poisson-

285 lognormal, in which observation-level random effects are used, or negative binomial (*glmer.nb*

286 function in package *lme4*). Nested random effects were included in global models where possible

12

287   because of the hierarchical nature of the study design. Where random effects explained none of

288   the variance, they were removed from models; this resulted in single random effects (rather than

289   nested) in some models (Table A.6). Model assumptions were verified by using standard model

290   check plots to assess the residuals for temporal and spatial dependency. Where necessary, square

291   root or log transformations of the response variable were used in linear mixed models (LMMs)

292   fitted by maximum likelihood. Model validation of all global models indicated no problems (except

293   in the phytometer 2013 global model which was not used, as explained below).

294   Global models were then used to generate all possible lower-dimensional models using the *MuMIn*

295   package (Bartoń, 2019). A subset of plausible 'top' models that explained the data best was chosen

296   from these candidate models using cut-off criteria for difference in AIC$_c$ (Δ_i) of 4 or less, always

297   ensuring that *S* (the number of models in the top models set) was less than the number of sites

298   used in the analysis (maximum *n* = 6) (Burnham et al., 2011; Grueber et al., 2011). AIC$_c$ was used

299   due to the small sample size. The 'top models' subset was then used for multi-model inference. This

300   model-averaging approach allowed us to explicitly incorporate the model selection uncertainty that

301   can result from small datasets, resulting in robust parameter estimates with reduced uncertainty

302   and bias (Burnham and Anderson, 2002; Grueber et al., 2011). Model-averaged parameters were

303   calculated using the natural average method (Burnham and Anderson, 2002).

304   It was necessary to use a negative binomial error structure for the hoverfly abundance dataset;

305   these models were not accepted by the *MuMIn* package, so candidate model sets were generated

306   by hand and then models were compared using package *AICcmodavg* (Mazerolle, 2019). Model

307   averaged parameters were then calculated from the top model set by hand (Equations A.1 – A.3,

308   Appendix A).

309   We would ideally have analysed the phytometer data from both years together, but the proposed

310   global model suffered from multicollinearity. This was due to the 2013 dataset, so we analysed the

311   two years separately (there were no correlation issues in the 2012 data). The proposed global

312   model for 2013 phytometer data (P-2013, Table A.6) was unusable due to multicollinearity (Table

313   B.12), and other variations of the model suffered from the same problem. These issues persisted

314   when we attempted to analyse each site separately. We could not, therefore, reliably use a linear

315   model for this analysis (Freckleton, 2011). Instead we carried out a Principal Components Analysis

316   (PCA) using the prcomp function in R core package 'stats'. The variables included in the PCA were

317   those originally identified as important when building the proposed global model. PCA is often used

318   to reduce the potential number of model parameters by selecting informative variables (King and

319   Jackson, 1999), but this was not possible here (see results).

320   When interpreting model-averaged results, the relative variable importance (w_{ip}) indicates the

321   strength of evidence for each variable. The larger the w_{ip} is, the more important that variable is

322   relative to the other predictor variables, and the more confidence we can have that it is a strong

323   predictor of the observed response. Predictor variables are considered important if $w_{ip} > 0.6$ and if

324   the confidence intervals do not overlap with zero (Burnham and Anderson, 2002). Unless stated

325   otherwise, model estimates are given at the mean of all other predictor variables.

326   **3. Results**

327   *3.1 Pollinator abundance*

328   *3.1.1 Bumblebee abundance*

329   Pollinator abundance on transect walks was higher in AF than MC treatments (Figure 1a). A total of

330   1,979 bumblebees were recorded on transect walks. After eliminating sampling occasions where

331   pasture sward structure or composition were incomparable (Appendix A), there were 1,159

332   bumblebees in total, of which 835 were recorded in the AF and 324 in the MC. The top models

333   subset and results of model averaging show that the variables with the largest effect on bumblebee

334   abundance are treatment, land use, and the interaction between these two (all have $w_{ip} = 1$ and CIs

335   do not include zero, Tables 1 & B.1). Of these three, the variable with the narrowest CI is treatment.

336   There is therefore strong evidence that treatment is an important (or even the most important)

14

337   predictor of bumblebee abundance. Model estimated bumblebee abundance on any given transect

338   was 1.8 in AF and 1.5 in MC. There is also very good evidence that the interaction between

339   treatment and land use is important: model estimated bumblebee abundance was 7.6 times

340   greater in silvoarable systems than in silvopasture systems (Figure 1a), and indeed model estimates

341   of bumblebee abundance showed no difference between treatments in the pasture systems. In

342   arable systems, model estimated bumblebee abundance was 2.4 times greater in AF than MC

343   (abundance per transect = 7.0 and 2.9 respectively). Bumblebee abundance was also affected by

344   the amount of sunshine during transects and distance to the nearest boundary hedgerow, with

345   fewer bumblebees observed further from boundary hedgerows (Table 1).

346   *3.1.2 Solitary bee abundance*

347   A total of 136 solitary bees were recorded on transects, of which 133 were seen in the AF

348   treatments and 7 in MC. Solitary bee abundance was higher in AF treatments than MC treatments

349   (w_{ip} treatment = 1, CIs do not include zero, Figure 1b, Tables 1 & B.2). Model estimated abundance

350   of solitary bees on any given transect was 1.4 in AF and 0.7 in MC. In addition, solitary bee numbers

351   were lower further from hedgerows and were affected by the amount of SNH in the landscape

352   (Tables 1 & B.2). As the amount of SNH in the surrounding landscape increased, numbers of solitary

353   bees in AF treatments were unaffected but numbers in MC treatments increased: an increase in

354   SNH from the mean of 11% to 35% resulted in more than a three-fold increase in numbers of

355   solitary bees in MC systems (from an average of 0.7 to 2.3 individuals on any given transect).

356   *3.1.3 Hoverfly abundance*

357   A total of 1,793 hoverflies were recorded on transects (after elimination of all data collected in

358   2011 from site WAF, see Methods). Of these, 1,332 individuals were recorded in AF and 461 in MC.

359   Hoverfly abundance was almost two times higher in AF than MC treatments (w_{ip} treatment = 1, CIs

360   do not include zero, Tables 1 & B.3, Figure 1c & d): model estimated abundance of hoverflies on

361   any given transect was 5.5 in AF and 2.8 in MC. Land use was also an important predictor (w_{ip} land

362   use = 1, CIs do not include zero, Tables 1 & B.3, Figure 1c & d): model estimated hoverfly

363   abundance on any given transect was three times higher in arable than in pasture land (8.3 and 2.7

364   respectively). Treatment had a slightly narrower CI than land use; there is therefore strong

365   evidence that treatment was an important (or even the most important) predictor of hoverfly

366   abundance. There is also weak evidence of an interaction between treatment and land use (Table

367   1): the AF treatment increased hoverfly abundance 2.9-fold in arable systems but only 1.6-fold in

368   pasture systems. Although there is weak evidence of an interaction effect, we plot hoverfly

369   abundance in arable and pasture land separately in Figure 1 because the far higher abundance in

370   arable land made an interaction plot hard to read. There is weak evidence that larger boundary

371   areas positively affected hoverfly abundance (Table 1). Date^2 also affected hoverfly abundance: this

372   is a known seasonal effect and the variable was included to improve model fit.

373   *3.2 Pollinator species richness (SR)*

374   In total, 178 bumblebee individuals from 11 species were caught in pan traps (after excluding data

375   from WAF 2011 and counting *Bombus terrestris* and *B. lucorum* as one aggregate species). All 11

376   species were found in AF treatments, and seven of these species were found in MC treatments. For

377   solitary bees, a total of 1,249 individuals were caught. After eliminating from the dataset all

378   unsuitable sampling occasions, then removing specimens in too poor a condition to identify (*n* = 6),

379   there were 1,133 solitary bee individuals comprising 57 solitary bee species from 11 genera. 50

380   species were recorded in AF and 36 species in MC. There is no evidence of a treatment effect on

381   either bumblebee or solitary bee SR: for both taxa, there is almost no difference between the best-

382   ranked model and the null model (Tables B.7 & B.8), indicating that they are almost equally as likely

383   as each other. Furthermore, treatment is not in any of the top bumblebee models (Tables 2 & B.7).

384   For both bumblebee and solitary bee SR, the predictor variables present in the top models subsets

385   either have CIs which include zero or/and they have very low w$_{ip}$ (Table 2). Solitary bee SR results

386   were obtained by extrapolating solitary bee data to *n*=14 sampling occasions; rarefaction to *n*=4

387   gave very similar results (Appendix B, Table B.9 & Figure B.1).

388 For both bumblebee and solitary bee SR the low Akaike weights of all the top models (Tables B.7 &

389 B.8) indicate high model-selection uncertainty, reducing our confidence in the data-based choice of

390 best models and reinforcing the need for multi-model inference (Burnham and Anderson, 2002). In

391 future, more data may enable identification of a 'best' model and/or stronger inference. Although

392 the data are not adequate to draw strong inference from the all-sites model, initial visualisation of

393 solitary bee SR data (although not bumblebee data) suggested a difference between treatments at

394 some sites. We therefore compared SR estimates at each site separately. This site-by-site analysis

395 (Figure 2) showed that extrapolated SR was significantly higher in the AF treatment at sites CE in

396 2011, at WH in 2011 and 2012, and at WAF in 2012 and 2013 (on average it was 10.5 times higher

397 in AF treatments). At WAF in 2011, LHF and SD the AF treatments had higher SR but not

398 significantly so. At one site (RR) the MC treatment had higher SR, although not significantly so

399 (Figure 2).

400 *3.3 Relationship between plant SR and higher trophic levels*

401 The effect of treatment on pollinator SR and abundance may be mediated through treatment

402 effects on plant SR. To investigate this relationship, we tested Pearson's product moment

403 correlation between plant SR and pollinator metrics. We found that plant SR and solitary bee SR

404 were positively correlated ($r_{(8)}$=0.67, p=0.04). No other pollinator metrics were correlated with

405 plant SR.

406 *3.4 Seed production*

407 Seed set in 2012 was higher in the AF treatment than in the MC treatment (w_{ip} treatment = 1, CIs

408 do not include zero, Tables 3 & B.11). From 36 plants (on each of which up to 20 buds were allowed

409 to develop), 335 seeds were produced. Of these, 239 seeds came from the AF treatment and 96

410 from the MC. Model estimated seed set was 0.9 seeds per fruit in AF and 0.2 in MC. Distance to the

411 nearest hedgerow affected seed set, with fewer seeds produced in phytometers further from

412   hedgerows. In AF treatments, for example, model estimated seed set 100m from the nearest hedge

413   was 0.6 seeds per fruit whereas at 20m it was 2.2 seeds per fruit.

414   In 2013 seed set was much higher per plant than in 2012: from 120 plants a total of 1,703 fruits

415   were produced, containing 58,297 seeds. Of these, 23,006 seeds were produced in the AF

416   treatment and 35,291 in MC. Mean number of seeds per fruit was 28 in AF and 39 in MC. We

417   investigated the relative effect of variables in the dataset using the first two principal components

418   from the PCA as they had eigenvalues greater than 1 and together explained 72.4% of the variance

419   (Figure 3, Table B.13). The three most representative variables on PCs 1 and 2 were the distance

420   between phytometers, followed by treatment and boundary area in joint second place (Figure B.3).

421   Figure 3 shows that different variables were important at different sites. At site WAF most of the

422   variance was on PC1. Distance between phytometers was the variable most significantly associated

423   ($p < 0.001$) with PC1. It had a correlation of 0.98, was the largest contributor to this component

424   (43%) and had the highest quality of representation (cos2 = 0.96) (Figure B.2, Table B.14). At WAF,

425   the phytometers were 2.5 times further apart in the AF treatment than in the MC treatment, and

426   the results indicate that this variable had a strong influence here. Treatment and hedge distance

427   were also significantly associated with PC1 (both $p < 0.001$) and were joint second in terms of both

428   contribution (each 24%) and quality (each cos2 = 0.54, Figure B.2, Table B.14): at WAF the hedges in

429   the AF were over twice as far from the phytometers as they were in MC. Figure 3 indicates that the

430   species richness of insect-pollinated plants in field boundaries was also a small contributor at WAF

431   (Figures B.2 & B.3), where it was higher in the MC treatment.

432   At the other two sites (LHF and SD), most of the variance was on PC2 (Figure 3). This component is

433   dominated by boundary area: its contribution and quality of representation were almost three

434   times greater than the next most important variable on PC2, which was treatment (Figures B.2 and

435   B.3, Table B.14). Both LHF and SD had large differences in the boundary areas of the two

436   treatments: at LHF the boundary area of the AF field was almost 3.5 times greater than in the MC;

437   at SD the boundary area of the AF field was 12.5 times smaller than in the MC.

438   Although PCA can be used to reduce the potential number of model parameters, a regression

439   analysis using the variables that contributed most to PCs 1 and 2 would be uninformative because

440   they are all correlated with each other (Table B.12). The PCA results indicate that other variables

441   were more important than treatment on both PCs, so we can draw no firm conclusions about the

442   effect of treatment on seed set in the phytometer 2013 dataset.

443   *3.5 Summary of results*

444   Without exception, in all multi-model inference analyses where there was evidence that one or

445   more variable(s) affected the response, treatment was the variable with the strongest evidence of

446   an effect. Therefore, presented below (Table 4) is a summary of treatment effects. The size and

447   direction of the effect is shown. Excluded from this summary are those analyses where there was

448   no strength of evidence for any variable affecting pollinators or pollination. We also exclude the

449   phytometer 2013 data.

450   Table 4 shows that overall, AF treatments had a positive effect on pollinators and pollination.

451   We highlight below some of the nuances in these results:

452   (i)   Solitary bee and hoverfly abundance were higher in AF treatments, regardless of land

453   use, whereas bumblebee abundance was higher in AF treatments in arable systems

454   only; in pasture systems bumblebees showed no evidence of a treatment effect.

455   (ii)   For bumblebees and hoverflies, the positive response to AF treatments was greater in

456   arable land than pastureland, although for hoverflies the evidence for this interaction

457   was only weak.

458   (iii) SR differences were harder to detect than abundance differences, and differences were

459   only observed at some sites.

460   (iv)   Only solitary bees showed a SR response to treatment; bumblebee SR showed no

461   response.

462   (v)   Plant SR was positively correlated with solitary bee SR, although not with any other

463   pollinator metrics.

4.   Discussion

4.1 Pollinator abundance

The higher abundance of all three wild pollinator taxa (bumblebees, solitary bees and hoverflies) in

AF compared to MC treatments is compelling evidence that modern AF systems in temperate

climates can support higher numbers of pollinators and thus potentially greater pollination service

than MC systems. This is supported by the 2012 phytometer results where we observed a

pronounced treatment effect, with 4.5 times higher seed set in AF than MC. This confirms that the

higher pollinator abundance in AF treatments in 2012 was being translated into increased

pollination service in these systems.

Our findings are consistent with the literature, a large body of which shows that insect abundance

displays strong local-scale responses to increased plant diversity (Lichtenberg et al., 2017). The

observed increase in pollinator abundance is likely to be because the AF treatments, particularly

the un-grazed ones, provided more floral, nesting and larval resources, more undisturbed areas,

and a more diverse sward structure. For solitary bees in particular, local-scale habitat

characteristics have been shown to have a strong influence on abundance (Hopfenmüller et al.,

2014; Scheper et al., 2015) and this group showed a very strong positive response to both the AF

treatment and proximity to hedgerows, which can be a good resource for wild bees (Garratt et al.,

2017; Ponisio et al., 2019).

We also found landscape-scale effects on solitary bees: in MC treatments, a higher percentage of

SNH in the surrounding landscape was related to higher solitary bee abundance, as observed

elsewhere (Bukovinszky et al., 2017; Nicholson et al., 2017). The fact that this effect only occurred

485   in MC treatments suggests that, for solitary bees, the influence of landscape-scale factors was

486   outweighed by local-scale factors (*i.e.* the AF treatment), in agreement with other studies

487   (Benjamin et al., 2014; Hopfenmüller et al., 2014). AF systems thus show great potential for

488   supporting and conserving solitary bees in UK farmland as well as providing greater levels of

489   pollination service.

490   Hoverfly abundance also exhibited a strong positive response to the AF treatment, in line with

491   findings that vegetation-structural traits and floral resource provision are important predictors of

492   hoverfly abundance (Bartual et al., 2019; Haenke et al., 2009). Pollination service provision by

493   hoverflies should therefore be higher in AF systems than in MC. Hoverfly abundance in both

494   treatments was higher in arable than pasture land, which is likely to be because many hoverflies

495   have aphidophagous larval stages so their abundance will be higher in land use types harbouring

496   aphid populations (Haenke et al., 2009). These findings thus suggest the potential for greater

497   natural pest control in AF systems, which has been observed in some AF systems elsewhere

498   (Pumariño et al., 2015; Staton et al., 2019); further work would be necessary to confirm this.

499   Both bumblebees and hoverflies showed a greater response to treatment in arable than pasture

500   land, in agreement with other studies which have observed greater effect sizes in arable (*i.e.* more

501   simplified) landscapes (Carvell et al., 2011; Haenke et al., 2009; Scheper et al., 2015). In our study,

502   the larger treatment effect in arable systems is likely to be due to the higher ecological contrast

503   created at these sites (Marja et al., 2019): most of the pasture systems were grazed, thus removing

504   understorey resources, whereas at arable sites the tree understoreys provided floral and nesting

505   resources and overwintering habitat, which promote pollinating insect abundance (Häussler et al.,

506   2017; Ramsden et al., 2015; Scheper et al., 2015). Incorporating fruit or nut trees into grazed

507   silvopasture systems could better support insect pollinator populations through increased floral

508   resources during the tree blossoming period (Häussler et al., 2017; Potts et al., 2009). Furthermore,

509   our pasture sites were grazed by sheep which crop the vegetation closely and create a homogenous

510   sward, reducing resources for pollinating insects. Other livestock, however, graze differently and so

511   there may be potentially greater resources for pollinating insects in other livestock systems

512   (Vanbergen et al., 2014, 2006). These factors highlight the need for careful design of AF systems,

513   ensuring that ecosystem service outcomes are explicitly planned right from the design stage rather

514   than being considered a coincidental bonus. Payments for Ecosystem Services schemes could help

515   focus attention on service provision at the planning stage, and this study provides the type of

516   quantitative evidence – linking land management to ecosystem service provision – that is required

517   when designing these schemes (DEFRA, 2014).

518   Pollinator activity was not recorded, so it is impossible to know whether the observed treatment

519   effect was having a population-level effect or simply attracting pollinators from elsewhere. It is,

520   however, possible that the increased pollinator abundance in AF systems may be at least partly due

521   to population-level effects as AF systems can provide many of the nesting and larval development

522   requirements of pollinators. Nevertheless, we can say with a high degree of confidence that the

523   higher pollinator abundance observed in AF treatments means that AF systems are a useful

524   resource for pollinators and can therefore support pollinator populations in the wider countryside.

525   *4.2   Pollinator species richness*

526   In contrast to pollinator abundance, pollinator SR did not exhibit such a pronounced treatment

527   effect (as also observed elsewhere, e.g. Bukovinszky et al. (2017)). Our confidence in the results of

528   the all-sites analyses was low and the results indicated a need for more data: it is thus likely that we

529   did not sample sufficiently to accurately estimate pollinator SR, which is known to be hard to

530   thoroughly sample especially over a small number of years (Russo et al., 2015). Increased sampling

531   effort would allow more robust analyses of treatment effects across sites in future.

532   Bumblebees and solitary bees differed in their response to treatment, as also found by others

533   (Kleijn and van Langevelde, 2006; Scheper et al., 2015): bumblebee SR showed no response to

534   treatment, whereas solitary bee SR was higher in the AF treatment in some years at three of the six

535   study sites. In agreement with other studies, we found different solitary bee SR responses in

536 grassland compared to arable land. One of the pasture sites with increased SR in the AF treatment

537 (site CE) also had the highest recorded amount of SNH in the surrounding landscape, concurring

538 with findings that agri-environmental management (AEM) in grassland has the greatest effect on

539 solitary bee SR in landscapes with more SNH (Concepción et al., 2012 - but see Kleijn and van

540 Langevelde, 2006). Conversely, the arable site that showed a treatment effect (site WH) was in a

541 highly homogenous, intensively-farmed region and had the least amount of SNH around it. This is in

542 line with studies showing that AEM in arable landscapes had the greatest effect on solitary bee SR

543 when there was little SNH in the surrounding landscape and where the management created large

544 local contrast in resources (Concepción et al., 2012; Holzschuh et al., 2007; Scheper et al., 2015).

545 The silvoarable system at WH provided great floral and structural diversity in the tree rows, thereby

546 creating a large ecological contrast: this was likely to be the driver of the observed SR increase

547 here.

548 The third site to show increased solitary bee SR in the AF treatment was another pasture site

549 (WAF), but this one was in a very intensively-farmed landscape with little SNH. It is possible that

550 here, the increased solitary bee SR may have been partly due to the fact that the site was un-grazed

551 and well-established (Table A.1), allowing the tree rows to develop a structurally complex

552 understorey that persisted from one year to the next (Buri et al., (2014) found cumulative (over

553 time) positive effects of uncut grass refugia on wild bee SR). Furthermore, it had the largest

554 contrast in within-field plant SR of any site, with over three times greater plant SR in the AF

555 treatment: we found that, across all sites, solitary bee SR was positively correlated with plant SR so

556 this may also have contributed to the observed difference in solitary bee SR at WAF. This

557 correlation between solitary bee and plant SR is in agreement with other findings (Isbell et al.,

558 2017; Lichtenberg et al., 2017; Sutter et al., 2017) and suggests that the treatment effect on SR was

559 due to the higher plant diversity in these systems. This once again highlights the importance of

560 careful design of AF systems to achieve the greatest possible increase in ecosystem service

561 provision and biodiversity conservation.

562   *4.3 Pollination service*

563   The 2012 phytometer experiment showed higher seed set and thus greater pollination service in AF

564   treatments, which is most likely to be due to the higher abundance of insect pollinators in AF

565   treatments. Our findings are in line with previous studies linking insect pollinator abundance to

566   pollination service (Winfree et al., 2015; Woodcock et al., 2019). The higher solitary bee SR in some

567   of the AF treatments may also have contributed, as species richness has been shown to support

568   pollination service (Albrecht et al., 2012; Dainese et al., 2019; Eeraerts et al., 2019) although its

569   contribution to service delivery is inferior to that of abundance (Kleijn et al., 2015).

570   The phytometer results were inconsistent across the two years, although it is likely that the

571   fieldwork issues in 2013 and experimental design were partly responsible, resulting in a very poor

572   quality dataset. The large difference in seed set in the two years is likely to have been because in

573   2012 there was one plant per position whereas in 2013 there were two plants per position. As *E.*

574   *californica* is self-incompatible, using a single plant per position is likely to have limited pollen

575   availability in 2012. Also, in 2013 the distance between phytometers was smaller in MC treatments

576   at two of the three sites (and equal in the third – hence its strong correlation with treatment in the

577   proposed global model, Table B.12). As seed set has been shown to increase at higher flower

578   densities (Dauber et al., 2010; Seifan et al., 2014) the distance between phytometers may have

579   caused density-dependent effects on pollination, resulting in higher seed set where phytometers

580   were closer together. Other variables likely to contribute indirectly to pollination (e.g. distance to

581   the nearest hedgerow, field boundary area) were also correlated with treatment in the 2013

582   proposed global model (Table B.12) and were shown to be more important than, or as important

583   as, treatment in the PCA. As a result, we cannot confidently ascribe the higher seed set in MC to

584   any one variable and we suggest re-doing the phytometer experiment to confirm the presence and

585   direction of any treatment effect. However, we remain confident in the conclusions drawn from the

586   2012 phytometer data.

5. Conclusions

This work presents strong empirical evidence that UK AF systems can support greater numbers of wild insect pollinators, greater pollination service and, at some sites, greater wild bee species richness. This could benefit both wild plant populations and insect pollinated agricultural crops in areas near AF systems. In Europe there is growing interest in the implementation of modern AF systems and this study provides robust evidence of its benefits to pollinators. These findings, taken together with evidence that AF systems can also produce more biomass per unit area than MC systems (Isbell et al., 2017; Sereke et al., 2015), means that AF systems may have a part to play in the sustainable intensification of agriculture. Our study adds to the body of evidence supporting the uptake of AF in temperate intensive farming systems. Our work also highlights that the provision of additional ecosystem services – *i.e.* ecosystem services other than biomass production – should be considered at the design stage of new AF systems to ensure the greatest possible benefit is realised.

Declaration of interest

The authors declare they have no conflicts of interest.

609 **6. References**

610 Albrecht, M., Schmid, B., Hautier, Y., Müller, C.B., Mu, C.B., 2012. Diverse pollinator communities

611   enhance plant reproductive success. Proc. R. Soc. London. Ser. B Biol. Sci. 279, 4845–4852.

612   doi:10.1098/rspb.2012.1621

613 Bartoń, K., 2019. Package "MuMIn": Multi-model inference. R package version 1.43.15.

614 Bartual, A.M., Sutter, L., Bocci, G., Moonen, A.-C., Cresswell, J., Entling, M., Giffard, B., Jacot, K.,

615   Jeanneret, P., Holland, J., Pfister, S., Pintér, O., Veromann, E., Winkler, K., Albrecht, M., 2019.

616   The potential of different semi-natural habitats to sustain pollinators and natural enemies in

617   European agricultural landscapes. Agric. Ecosyst. Environ. 279, 43–52.

618   doi:10.1016/J.AGEE.2019.04.009

619 Batáry, P., Dicks, L. V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in

620   conservation and environmental management. Conserv. Biol. 29, 1006–1016.

621   doi:10.1111/cobi.12536

622 Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using

623   lme4. J. Stat. Softw. 67, 1–48.

624 Benjamin, F.E., Reilly, J.R., Winfree, R., 2014. Pollinator body size mediates the scale at which land

625   use drives crop pollination services. J. Appl. Ecol. 51, 440–449. doi:10.1111/1365-2664.12198

626 Borer, E.T., Seabloom, E.W., Tilman, D., 2012. Plant diversity controls arthropod biomass and

627   temporal stability. Ecol. Lett. 15, 1457–1464. doi:10.1111/ele.12006

628 Breeze, T.D., Bailey, A.P., Balcombe, K.G., Potts, S.G., 2011. Pollination services in the UK: How

629   important are honeybees? Agric. Ecosyst. Environ. 142, 137–143.

630   doi:10.1016/J.AGEE.2011.03.020

631 Briggs, H.M., Perfecto, I., Brosi, B.J., 2013. The Role of the Agricultural Matrix: Coffee Management

632   and Euglossine Bee (Hymenoptera: Apidae: Euglossini) Communities in Southern Mexico.

633   Environ. Entomol. 42, 1210–1217. doi:10.1603/en13087

634   Bukovinszky, T., Verheijen, J., Zwerver, S., Klop, E., Biesmeijer, J.C., Wäckers, F.L., Prins, H.H.T.,

635   Kleijn, D., 2017. Exploring the relationships between landscape complexity, wild bee species

636   richness and reproduction, and pollination services along a complexity gradient in the

637   Netherlands. Biol. Conserv. 214, 312–319. doi:10.1016/J.BIOCON.2017.08.027

638   Buri, P., Humbert, J.-Y., Arlettaz, R., 2014. Promoting Pollinating Insects in Intensive Agricultural

639   Matrices: Field-Scale Experimental Manipulation of Hay-Meadow Mowing Regimes and Its

640   Effects on Bees. PLoS One 9, e85635. doi:10.1371/journal.pone.0085635

641   Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. A Practical

642   Information-Theoretic Approach, Second. ed. Springer, New York.

643   Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference

644   in behavioral ecology: some background, observations, and comparisons. Behav. Ecol.

645   Sociobiol. 65, 23–35. doi:10.1007/s00265-010-1029-6

646   Butler, S.J., Brooks, D., Feber, R.E., Storkey, J., Vickery, J.A., Norris, K., 2009. A cross-taxonomic

647   index for quantifying the health of farmland biodiversity. J. Appl. Ecol. 46, 1154–1162.

648   doi:10.1111/j.1365-2664.2009.01709.x

649   Campbell, J.W., Hanula, J.L., 2007. Efficiency of Malaise traps and colored pan traps for collecting

650   flower visiting insects from three forested ecosystems. J. Insect Conserv. 11, 399–408.

651   doi:10.1007/s10841-006-9055-4

652   Carvell, C., Osborne, J.L., Bourke, A.F.G., Freeman, S.N., Pywell, R.F., Heard, M.S., 2011. Bumble bee

653   species' responses to a targeted conservation measure depend on landscape context and

654   habitat quality. Ecol. Appl. 21, 1760–1771. doi:10.1890/10-0677.1

655   Castle, D., Grass, I., Westphal, C., 2019. Fruit quantity and quality of strawberries benefit from

656   enhanced pollinator abundance at hedgerows in agricultural landscapes. Agric. Ecosyst.

27

657   Environ. 275, 14–22. doi:10.1016/j.agee.2019.01.003

658   Colwell, R.K., 2013. EstimateS: Statistical estimation of species richness and shared species from

659   samples. User's Guide and application published at: http://purl.oclc.org/estimates.

660   Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F.,

661   Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2012. Interactive effects of

662   landscape context constrain the effectiveness of local agri-environmental management. J.

663   Appl. Ecol. 49, 695–705. doi:10.1111/j.1365-2664.2012.02131.x

664   Dainese, M., Martin, E.A., Aizen, M., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G.,

665   Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D.S.,

666   Kennedy, C.M., Kleijn, D., Kremen, C., Landis, D.A., Letourneau, D.K., Marini, L., Poveda, K.,

667   Rader, R., Smith, H.G., Tscharntke, T., Andersson, G.K.S., Badenhausser, I., Baensch, S.,

668   Bezerra, A.D.M., Bianchi, F.J.J.A., Boreux, V., Bretagnolle, V., Caballero-Lopez, B., Cavigliasso,

669   P., Cetkovic, A., Chacoff, N.P., Classen, A., Cusser, S., Silva, F.D. da S. e, Groot, G.A. de,

670   Dudenhoffer, J.H., Ekroos, J., Fijen, T., Franck, P., Freitas, B.M., Garratt, M.P.D., Gratton, C.,

671   Hipolito, J., Holzschuh, A., Hunt, L., Iverson, A.L., Jha, S., Keasar, T., Kim, T.N., Kishinevsky, M.,

672   Klatt, B.K., Klein, A., Krewenka, K.M., Krishnan, S., Larsen, A.E., Lavigne, C., Leire, H., Maas, B.,

673   Nesper, M., Mallinger, R.E., Martinez, E., Martinez-Salinas, A., Meehan, T.D., Mitchell, M.G.E.,

674   Molina, G.A.R., Nilsson, L., O'Rourke, M., Peters, M.K., Plecas, M., Potts, Si.G., Ramos, D. de L.,

675   Rosenheim, J.A., Rundlof, M., Rusch, A., Saez, A., Scheper, J., Schleuning, M., Schmack, J.,

676   Sciligo, A.R., Seymour, C., Stanley, D.A., Stewart, R., Stout, J.C., Sutter, L., Takada, M.B., Taki,

677   H., Tamburini, G., Tschumi, M., Viana, B.F., Westphal, C., Wilcox, B.K., Wratten, S.D., Yoshioka,

678   A., Zaragoza, C., Zhang, W., Zou, Y., Steffan-Dewenter, I., 2019. A global synthesis reveals

679   biodiversity-mediated benefits for crop production. Sci. Adv. 5, eaax0121.

680   doi:10.1126/sciadv.aax0121

681   Dauber, J., Biesmeijer, J.C., Gabriel, D., Kunin, W.E., Lamborn, E., Meyer, B., Nielsen, A., Potts, S.G.,

682   Roberts, S.P.M., Sõber, V., Settele, J., Steffan-Dewenter, I., Stout, J.C., Teder, T., Tscheulin, T.,

683   Vivarelli, D., Petanidou, T., 2010. Effects of patch size and density on flower visitation and

684   seed set of wild plants: A pan-European approach. J. Ecol. 98, 188–196. doi:10.1111/j.1365-

685   2745.2009.01590.x

686   DEFRA, 2014. Defra Payments for Ecosystem Services (PES) Pilot Projects : Review of key findings

687   2011–2013.

688   Deguines, N., Jono, C., Baude, M., Henry, M., Julliard, R., Fontaine, C., 2014. Large-scale trade-off

689   between agricultural intensification and crop pollination services. Front. Ecol. Environ. 12,

690   212–217. doi:10.1890/130054

691   Dicks, L. V., Bardgett, R.D., Bell, J., Benton, T.G., Booth, A., Bouwman, J., Brown, C., Bruce, A.,

692   Burgess, P.J., Butler, S.J., Crute, I., Dixon, F., Drummond, C., Freckleton, R.P., Gill, M., Graham,

693   A., Hails, R.S., Hallett, J., Hart, B., Hillier, J.G., Holland, J.M., Huxley, J.N., Ingram, J.S.I., King, V.,

694   MacMillan, T., McGonigle, D.F., McQuaid, C., Nevard, T., Norman, S., Norris, K., Pazderka, C.,

695   Poonaji, I., Quinn, C.H., Ramsden, S.J., Sinclair, D., Siriwardena, G.M., Vickery, J.A., Whitmore,

696   A.P., Wolmer, W., Sutherland, W.J., 2013. What do we need to know to enhance the

697   environmental sustainability of agricultural production? A prioritisation of knowledge needs

698   for the UK food system. Sustain. 5, 3095–3115. doi:10.3390/su5073095

699   Eeraerts, M., Smagghe, G., Meeus, I., 2019. Pollinator diversity, floral resources and semi-natural

700   habitat, instead of honey bees and intensive agriculture, enhance pollination service to sweet

701   cherry. Agric. Ecosyst. Environ. 284. doi:10.1016/j.agee.2019.106586

702   Elliott, L.P., Brook, B.W., 2007. Revisiting Chamberlin: Multiple Working Hypotheses for the 21st

703   Century. Bioscience 57, 608–614. doi:10.1641/b570708

704   Fijen, T.P.M., Scheper, J.A., Boom, T.M., Janssen, N., Raemakers, I., Kleijn, D., 2018. Insect

705   pollination is at least as important for marketable crop yield as plant quality in a seed crop.

706   Ecol. Lett. 21, 1704–1713. doi:10.1111/ele.13150

707 Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T.,

708   Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda,

709   C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global Consequences of Land

710   Use. Science (80-.). 309, 570–574. doi:10.1126/science.1111772

711 Freckleton, R.P., 2011. Dealing with collinearity in behavioural and ecological data: Model averaging

712   and the problems of measurement error. Behav. Ecol. Sociobiol. 65, 91–101.

713   doi:10.1007/s00265-010-1045-6

714 Gabriel, D., Sait, S.M., Kunin, W.E., Benton, T.G., 2013. Food production vs. biodiversity: comparing

715   organic and conventional agriculture. J. Appl. Ecol. 50, 355–364. doi:10.1111/1365-

716   2664.12035

717 Garibaldi, L.A., Aizen, M.A., Klein, A.M., Cunningham, S.A., Harder, L.D., 2011a. Global growth and

718   stability of agricultural yield decrease with pollinator dependence. Proc. Natl. Acad. Sci. U. S.

719   A. 108, 5909–14. doi:10.1073/pnas.1012431108

720 Garibaldi, L.A., Gemmill-Herren, B., D'Annolfo, R., Graeub, B.E., Cunningham, S.A., Breeze, T.D.,

721   2016. Farming Approaches for Greater Biodiversity, Livelihoods, and Food Security. Trends

722   Ecol. Evol. 32, 68–80. doi:10.1016/j.tree.2016.10.001

723 Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A.,

724   Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V.,

725   Cariveau, D., Chacoff, N.P., Dudenhoffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipolito,

726   J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M.,

727   Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M.,

728   Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlof, M., Seymour, C.L.,

729   Schuepp, C., Szentgyorgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C.,

730   Westphal, C., Williams, N., Klein, A.M., 2013. Wild Pollinators Enhance Fruit Set of Crops

731   Regardless of Honey Bee Abundance. Science (80-.). 339, 1608–1611.

732 doi:10.1126/science.1230200

733 Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A.,

734 Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R.,

735 Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H.,

736 Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011b. Stability of

737 pollination services decreases with isolation from natural areas despite honey bee visits. Ecol.

738 Lett. 14, 1062–1072. doi:10.1111/J.1461-0248.2011.01669.X@10.1111/(ISSN)1461-

739 0248.ANTHROPOGENIC-CHANGE

740 Garratt, M.P.D., Breeze, T.D., Jenner, N., Polce, C., Biesmeijer, J.C., Potts, S.G., 2014. Avoiding a bad

741 apple: Insect pollination enhances fruit quality and economic value. Agric. Ecosyst. Environ.

742 184, 34–40. doi:10.1016/J.AGEE.2013.10.032

743 Garratt, M.P.D., Senapathi, D., Coston, D.J., Mortimer, S.R., Potts, S.G., 2017. The benefits of

744 hedgerows for pollinators and natural enemies depends on hedge quality and landscape

745 context. Agric. Ecosyst. Environ. 247, 363–370. doi:10.1016/j.agee.2017.06.048

746 Gelman, A., Su, Y.-S., Yajima, M., Hill, J., Pittau, M.G., Kerman, J., Zheng, T., Dorie, V., 2013. Package

747 "arm". Data Analysis Using Regression and Multilevel/Hierarchical Models.

748 Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress

749 from parasites, pesticides, and lack of flowers. Science 347, 1255957.

750 doi:10.1126/science.1255957

751 Grab, H., Branstetter, M.G., Amon, N., Urban-Mead, K.R., Park, M.G., Gibbs, J., Blitzer, E.J., Poveda,

752 K., Loeb, G., Danforth, B.N., 2019. Agriculturally dominated landscapes reduce bee

753 phylogenetic diversity and pollination services. Science (80-.). 363, 282–284.

754 doi:10.1126/SCIENCE.AAT6016

755 Greenleaf, S.S., Williams, N.M., Kremen, C., 2007. Bee foraging ranges and their relationship to

756   body size. Source: Oecologia 153, 589–596. doi:10.1007/s00442-007

757 Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and

758   evolution: challenges and solutions. J. Evol. Biol. 24, 699–711. doi:10.1111/j.1420-

759   9101.2010.02210.x

760 Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T., Thies, C., 2009. Increasing syrphid fly diversity

761   and density in sown flower strips within simple vs. complex landscapes. J. Appl. Ecol. 46,

762   1106–1114. doi:10.1111/j.1365-2664.2009.01685.x

763 Hardman, C.J., Norris, K., Nevard, T.D., Hughes, B., Potts, S.G., 2016. Delivery of floral resources and

764   pollination services on farmland under three different wildlife-friendly schemes. Agric.

765   Ecosyst. Environ. 220, 142–151. doi:10.1016/j.agee.2016.01.015

766 Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson,

767   B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-

768   model inference in ecology. PeerJ 2018. doi:10.7717/peerj.4794

769 Hass, A.L., Liese, B., Heong, K.L., Settele, J., Tscharntke, T., Westphal, C., 2018. Plant-pollinator

770   interactions and bee functional diversity are driven by agroforests in rice-dominated

771   landscapes. Agric. Ecosyst. Environ. 253, 140–147. doi:10.1016/J.AGEE.2017.10.019

772 Häussler, J., Sahlin, U., Baey, C., Smith, H.G., Clough, Y., 2017. Pollinator population size and

773   pollination ecosystem service responses to enhancing floral and nesting resources. Ecol. Evol.

774   doi:10.1002/ece3.2765

775 Hoehn, P., Steffan-Dewenter, I., Tscharntke, T., 2012. Relative contribution of agroforestry,

776   rainforest and openland to local and regional bee diversity. Biodivers. Conserv. 19, 2189–

777   2200. doi:10.1007/s10531-010-9831-z

778 Hoehn, P., Tscharntke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of

779   bee pollinators increases crop yield. Proc. R. Soc. B Biol. Sci. 275, 2283–2291.

780   doi:10.1098/rspb.2008.0405

781   Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tscharntke, T., 2007. Diversity of flower-visiting bees

782   in cereal fields: effects of farming system, landscape composition and regional context. J.

783   Appl. Ecol. 44, 41–49. doi:10.1111/j.1365-2664.2006.01259.x

784   Hopfenmüller, S., Steffan-Dewenter, I., Holzschuh, A., 2014. Trait-specific responses of wild bee

785   communities to landscape composition, configuration and local factors. PLoS One 9.

786   doi:10.1371/journal.pone.0104439

787   IPBES, 2019. Global Assessment Report on Biodiversity and Ecosystem Services | IPBES. IPBES

788   secretariat, Bonn, Germany.

789   Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., Letourneau, D.K., Liebman,

790   M., Polley, H.W., Quijas, S., Scherer-Lorenzen, M., 2017. Benefits of increasing plant diversity

791   in sustainable agroecosystems. J. Ecol. 105, 871–879. doi:10.1111/1365-2745.12789

792   Jennersten, O., 1984. Flower visitation and pollination efficiency of some North European

793   butterflies. Oecologia 63, 80–89. doi:10.1007/BF00379789

794   Jose, S., 2009. Agroforestry for ecosystem services and environmental benefits: an overview.

795   Agrofor. Syst. 76, 1–10. doi:10.1007/s10457-009-9229-7

796   Kallioniemi, E., Åström, J., Rusch, G.M., Dahle, S., Åström, S., Gjershaug, J.O., 2017. Local resources,

797   linear elements and mass-flowering crops determine bumblebee occurrences in moderately

798   intensified farmlands. Agric. Ecosyst. Environ. 239, 90–100. doi:10.1016/J.AGEE.2016.12.039

799   Kay, S., Crous-Duran, J., Ferreiro-Domínguez, N., García de Jalón, S., Graves, A., Moreno, G.,

800   Mosquera-Losada, M.R., Palma, J.H.N., Roces-Díaz, J. V., Santiago-Freijanes, J.J., Szerencsits,

801   E., Weibel, R., Herzog, F., 2018. Spatial similarities between European agroforestry systems

802   and ecosystem services at the landscape scale. Agrofor. Syst. 92, 1075–1089.

803   doi:10.1007/s10457-017-0132-3

804   Kay, S., Kühn, E., Albrecht, M., Sutter, L., Szerencsits, E., Herzog, F., 2019. Agroforestry can enhance

805   foraging and nesting resources for pollinators with focus on solitary bees at the landscape

806   scale. Agrofor. Syst. 1–9. doi:10.1007/s10457-019-00400-9

807   King, J.R., Jackson, D.A., 1999. Variable selection in large environmental data sets using principal

808   components analysis. Environmetrics 10, 67–77. doi:10.1002/(SICI)1099-

809   095X(199901/02)10:1<67::AID-ENV336>3.0.CO;2-0

810   Klatt, B.K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E., Tscharntke, T., 2013. Bee

811   pollination improves crop quality, shelf life and commercial value. Proc. R. Soc. B Biol. Sci. 281.

812   doi:10.1098/rspb.2013.2440

813   Kleijn, D., van Langevelde, F., 2006. Interacting effects of landscape context and habitat quality on

814   flower visiting insects in agricultural landscapes. Basic Appl. Ecol. 7, 201–214.

815   doi:http://dx.doi.org/10.1016/j.baae.2005.07.011

816   Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen,

817   C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S.,

818   Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R.,

819   Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E.,

820   Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka,

821   K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V.,

822   Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter,

823   I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Westphal, C.,

824   Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild

825   pollinator conservation. Nat. Commun. 6. doi:10.1038/ncomms8414

826   Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C.,

827   Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc.

828   R. Soc. B Biol. Sci. 274, 303–313. doi:10.1098/rspb.2006.3721

829   Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A.J., Settele, J., Kremen, C., Dicks, L. V., 2017.

830   Ecological intensification to mitigate impacts of conventional intensive land use on pollinators

831   and pollination. Ecol. Lett. doi:10.1111/ele.12762

832   Kuyah, S., Öborn, I., Jonsson, M., 2017. Regulating Ecosystem Services Delivered in Agroforestry

833   Systems, in: Dagar, J.C., Tewari, V.P. (Eds.), Agroforestry: Anecdotal to Modern Science.

834   Springer Singapore, Singapore, pp. 797–815. doi:10.1007/978-981-10-7650-3_33

835   Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-

836   Pérez, N.A., Carvalheiro, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Åström, S.,

837   Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T.,

838   Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H.,

839   Gratton, C., Holzschuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A.-M.,

840   Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martinez, E.,

841   Memmott, J., Morandin, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Pocock, M.J.O.,

842   Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlöf, M., Sardiñas, H.,

843   Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tscharntke, T.,

844   Veselý, M., Weisser, W.W., Wilson, J.K., Crowder, D.W., 2017. A global synthesis of the effects

845   of diversified farming systems on arthropod diversity within fields and across agricultural

846   landscapes. Glob. Chang. Biol. doi:10.1111/gcb.13714

847   Lin, M., Huybers, P., 2012. Reckoning wheat yield trends. Environ. Res. Lett. 7, 024016.

848   doi:10.1088/1748-9326/7/2/024016

849   Marja, R., Kleijn, D., Tscharntke, T., Klein, A., Frank, T., Batáry, P., 2019. Effectiveness of agri-

850   environmental management on pollinators is moderated more by ecological contrast than by

851   landscape structure or land-use intensity. Ecol. Lett. ele.13339. doi:10.1111/ele.13339

852   Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M.P.D., Holzschuh,

853   A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S.G., Smith, H.G., Al Hassan, D.,

854 Albrecht, M., Andersson, G.K.S., Asís, J.D., Aviron, S., Balzan, M. V., Baños-Picón, L.,

855 Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E.D., Coudrain, V.,

856 Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C.F., Duflot, R., Entling, M.H., Farwig, N.,

857 Fischer, C., Frank, T., Garibaldi, L.A., Hermann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F.,

858 Jeanneret, P., Kaiser, M., Krauss, J., Le Féon, V., Marshall, J., Moonen, A., Moreno, G.,

859 Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter,

860 L., Tamburini, G., Thies, C., Tormos, J., Tscharntke, T., Tschumi, M., Uzman, D., Wagner, C.,

861 Zubair-Anjum, M., Steffan-Dewenter, I., 2019. The interplay of landscape composition and

862 configuration: new pathways to manage functional biodiversity and agroecosystem services

863 across Europe. Ecol. Lett. 22, 1083–1094. doi:10.1111/ele.13265

864 Mazerolle, M.J., 2019. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).

865 R package version 2.2-2.

866 Meyer, C., 2012. Agroforestry: A study of farmer attitudes and perceptions in England. MSc thesis.

867 University of Reading.

868 Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J.,

869 Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J.,

870 Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J.,

871 Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan,

872 Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J.,

873 Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on

874 local terrestrial biodiversity. Nature 520, 45–50. doi:10.1038/nature14324

875 Nicholls, C., Altieri, M., 2013. Plant biodiversity enhances bees and other insect pollinators in

876 agroecosystems. A review. Agron. Sustain. Dev. 33, 257–274. doi:10.1007/s13593-012-0092-y

877 Nicholson, C.C., Koh, I., Richardson, L.L., Beauchemin, A., Ricketts, T.H., 2017. Farm and landscape

878 factors interact to affect the supply of pollination services. Agric. Ecosyst. Environ. 250, 113–

879   122. doi:10.1016/J.AGEE.2017.08.030

880   O'Connor, R.S., Kunin, W.E., Garratt, M.P.D., Potts, S.G., Roy, H.E., Andrews, C., Jones, C.M., Peyton,

881   J., Savage, J., Harvey, M., Morris, R.K.A., Roberts, S.P.M., Wright, I., Vanbergen, A.J., Carvell, C.,

882   2019. Monitoring insect pollinators and flower visitation: the effectiveness and feasibility of

883   different survey methods. Methods Ecol. Evol. 2041–210X.13292. doi:10.1111/2041-

884   210X.13292

885   Peng, R.K., Incoll, L.D., Sutton, S.L., Wright, C., Chadwick, A., 1993. Diversity of Airborne Arthropods

886   in a Silvoarable Agroforestry System. J. Appl. Ecol. 30, 551–562.

887   Persson, A.S., Rundlof, M., Clough, Y., Smith, H.G., 2015. Bumble bees show trait-dependent

888   vulnerability to landscape simplification. Biodivers. Conserv. 24, 3469–3489.

889   doi:10.1007/s10531-015-1008-3

890   Ponisio, L.C., de Valpine, P., M'Gonigle, L.K., Kremen, C., 2019. Proximity of restored hedgerows

891   interacts with local floral diversity and species' traits to shape long-term pollinator

892   metacommunity dynamics. Ecol. Lett. 22, ele.13257. doi:10.1111/ele.13257

893   Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global

894   pollinator declines: Trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353.

895   doi:10.1016/j.tree.2010.01.007

896   Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L. V,

897   Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their

898   values to human well-being. Nature 540, 220–229. doi:10.1038/nature20588

899   Potts, S.G., Woodcock, B.A., Roberts, S.P.M., Tscheulin, T., Pilgrim, E.S., Brown, V.K., Tallowin, J.R.,

900   2009. Enhancing pollinator biodiversity in intensive grasslands. J. Appl. Ecol. 46, 369–379.

901   doi:10.1111/j.1365-2664.2009.01609.x

902   Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., Isaac, N.J.B., 2019.

903   Widespread losses of pollinating insects in Britain. Nat. Commun. 10, 1018.

904   doi:10.1038/s41467-019-08974-9

905   Pretty, J., Benton, T.G., Bharucha, Z.P., Dicks, L. V., Flora, C.B., Godfray, H.C.J., Goulson, D., Hartley,

906   S., Lampkin, N., Morris, C., Pierzynski, G., Prasad, P.V.V., Reganold, J., Rockström, J., Smith, P.,

907   Thorne, P., Wratten, S., 2018. Global assessment of agricultural system redesign for

908   sustainable intensification. Nat. Sustain. 1, 441–446. doi:10.1038/s41893-018-0114-0

909   Pumariño, L., Sileshi, G.W., Gripenberg, S., Kaartinen, R., Barrios, E., Muchane, M.N., Midega, C.,

910   Jonsson, M., 2015. Effects of agroforestry on pest, disease and weed control: A meta-analysis.

911   Basic Appl. Ecol. 16, 573–582. doi:10.1016/j.baae.2015.08.006

912   R Development Core Team, 2019. R: A language and environment for statistical computing.

913   Ramsden, M.W., Menéndez, R., Leather, S.R., Wäckers, F., 2015. Optimizing field margins for

914   biocontrol services: The relative role of aphid abundance, annual floral resources, and

915   overwinter habitat in enhancing aphid natural enemies. Agric. Ecosyst. Environ. 199, 94–104.

916   doi:10.1016/j.agee.2014.08.024

917   Ray, D.K., Ramankutty, N., Mueller, N.D., West, P.C., Foley, J.A., 2012. Recent patterns of crop yield

918   growth and stagnation. Nat Commun 3, 1293.

919   doi:http://www.nature.com/ncomms/journal/v3/n12/suppinfo/ncomms2296_S1.html

920   Rhodes, T.K., Aguilar, F.X., Jose, S., Gold, M., 2018. Factors influencing the adoption of riparian

921   forest buffers in the Tuttle Creek Reservoir watershed of Kansas, USA. Agrofor. Syst. 92, 739–

922   757. doi:10.1007/s10457-016-0045-6

923   Rockström, J., Williams, J., Daily, G., Noble, A., Matthews, N., Gordon, L., Wetterstrand, H.,

924   DeClerck, F., Shah, M., Steduto, P., de Fraiture, C., Hatibu, N., Unver, O., Bird, J., Sibanda, L.,

925   Smith, J., 2017. Sustainable intensification of agriculture for human prosperity and global

926   sustainability. Ambio 46, 4–17. doi:10.1007/s13280-016-0793-6

927   Roulston, T.H., Goodell, K., 2011. The Role of Resources and Risks in Regulating Wild Bee

928   Populations. Annu. Rev. Entomol. 56, 293–312. doi:10.1146/annurev-ento-120709-144802

929   Russo, L., Park, M., Gibbs, J., Danforth, B., 2015. The challenge of accurately documenting bee

930   species richness in agroecosystems: bee diversity in eastern apple orchards. Ecol. Evol. 5,

931   3531–3540. doi:10.1002/ece3.1582

932   Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its

933   drivers. Biol. Conserv. 232, 8–27. doi:10.1016/J.BIOCON.2019.01.020

934   Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M.,

935   Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleijn, D., 2015. Local and

936   landscape-level floral resources explain effects of wildflower strips on wild bees across four

937   European countries. J. Appl. Ecol. 52, 1165–1175. doi:10.1111/1365-2664.12479

938   Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013.

939   Environmental factors driving the effectiveness of European agri-environmental measures in

940   mitigating pollinator loss – a meta-analysis. Ecol. Lett. 16, 912–920. doi:10.1111/ele.12128

941   Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D.,

942   Roscher, C., Weigelt, A., Allan, E., Beszler, H., Bonkowski, M., Buchmann, N., Buscot, F.,

943   Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.-M., Koller, R., Konig, S.,

944   Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.D.,

945   Milcu, A., Muller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S.,

946   Schumacher, J., Temperton, V.M., Tscharntke, T., 2010. Bottom-up effects of plant diversity on

947   multitrophic interactions in a biodiversity experiment. Nature 468, 553–556.

948   doi:http://www.nature.com/nature/journal/v468/n7323/abs/nature09492.html#supplement

949   ary-information

950   Seifan, M., Hoch, E.M., Hanoteaux, S., Tielbörger, K., 2014. The outcome of shared pollination

951   services is affected by the density and spatial pattern of an attractive neighbour. J. Ecol. 102,

952   953–962. doi:10.1111/1365-2745.12256

953 Sereke, F., Graves, A.R., Dux, D., Palma, J.H.N., Herzog, F., 2015. Innovative agroecosystem goods

954   and services: key profitability drivers in Swiss agroforestry. Agron. Sustain. Dev. 35, 759–770.

955   doi:10.1007/s13593-014-0261-2

956 Smith, J., Pearce, B.D., Wolfe, M.S., 2012. A European perspective for developing modern

957   multifunctional agroforestry systems for sustainable intensification. Renew. Agric. Food Syst.

958   27, 323–332. doi:10.1017/S1742170511000597

959 Smith, P., Ashmore, M., Black, H., Burgess, P., Evans, C., Hails, R., Potts, S.G., Thomson, A., Quine, T.,

960   Biesmeijer, K., Breeze, T., Broadmeadow, M., Ferrier, R., Freer, J., Hansom, J., Haygarth, P.,

961   Hesketh, H., Hicks, K., Johnson, A., Kay, D., Kunin, W., Lilly, A., May, L., Memmott, J., Orr, H.,

962   Pickup, R., Purse, B., Squire, G., 2011. Regulating services [chapter 14], in: UK National

963   Ecosystem Assessment. Understanding Nature's Value to Society. Technical Report. UNEP-

964   WCMC, Cambridge, UK, pp. 535–596.

965 Staton, T., Walters, R.J., Smith, J., Girling, R.D., 2019. Evaluating the effects of integrating trees into

966   temperate arable systems on pest control and pollination. Agric. Syst. 176, 102676.

967   doi:10.1016/j.agsy.2019.102676

968 Sutter, L., Jeanneret, P., Bartual, A.M., Bocci, G., Albrecht, M., 2017. Enhancing plant diversity in

969   agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through

970   complementary increase in key floral resources. J. Appl. Ecol. doi:10.1111/1365-2664.12907

971 Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and

972   model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol.

973   Sociobiol. 65, 13–21. doi:10.1007/s00265-010-1037-6

974 Valdivia, C., Barbieri, C., Gold, M.A., 2012. Between Forestry and Farming: Policy and Environmental

975   Implications of the Barriers to Agroforestry Adoption. Can. J. Agric. Econ. Can. d'agroeconomie

976   60, 155–175. doi:10.1111/j.1744-7976.2012.01248.x

977   Vanbergen, A.J., Hails, R.S., Watt, A.D., Jones, T.H., 2006. Consequences for host-parasitoid

978   interactions of grazing-dependent habitat heterogeneity. J. Anim. Ecol. 75, 789–801.

979   doi:10.1111/j.1365-2656.2006.01099.x

980   Vanbergen, A.J., the IPI, 2013. Threats to an ecosystem service: pressures on pollinators. Front.

981   Ecol. Environ. 11, 251–259. doi:10.1890/120126

982   Vanbergen, A.J., Woodcock, B.A., Gray, A., Grant, F., Telford, A., Lambdon, P., Chapman, D.S.,

983   Pywell, R.F., Heard, M.S., Cavers, S., 2014. Grazing alters insect visitation networks and plant

984   mating systems. Funct. Ecol. 28, 178–189. doi:10.1111/1365-2435.12191

985   Vandermeer, J., Perfecto, I., 2007. The agricultural matrix and a future paradigm for conservation.

986   Conserv. Biol. 21, 274–277. doi:DOI: 10.1111/j.1523-1739.2006.00582.x

987   Varah, A., Jones, H., Smith, J., Potts, S.G., 2013. Enhanced biodiversity and pollination in UK

988   agroforestry systems. J. Sci. Food Agric. 93, 2073–2075. doi:10.1002/jsfa.6148

989   Winfree, R., Reilly, J.R., Bartomeus, I., Cariveau, D.P., Williams, N.M., Gibbs, J., 2018. Species

990   turnover promotes the importance of bee diversity for crop pollination at regional scales.

991   Science (80-.). 359, 791–793. doi:10.1126/SCIENCE.AAO2117

992   Winfree, R., W. Fox, J., Williams, N.M., Reilly, J.R., Cariveau, D.P., 2015. Abundance of common

993   species, not species richness, drives delivery of a real-world ecosystem service. Ecol. Lett. 18,

994   626–635. doi:10.1111/ele.12424

995   Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J., Lindström,

996   S.A.M., Stanley, D., Ouvrard, P., Edwards, M.E., Jauker, F., McCracken, M.E., Zou, Y., Potts,

997   S.G., Rundlöf, M., Noriega, J.A., Greenop, A., Smith, H.G., Bommarco, R., van der Werf, W.,

998   Stout, J.C., Steffan-Dewenter, I., Morandin, L., Bullock, J.M., Pywell, R.F., 2019. Meta-analysis

999   reveals that pollinator functional diversity and abundance enhance crop pollination and yield.

1000   Nat. Commun. 10. doi:10.1038/s41467-019-09393-6

1001   Woodcock, T.S., Pekkola, L.J., Dawson, C., Gadallah, F.L., Kevan, P.G., 2014. Development of a

1002   Pollination Service Measurement (PSM) method using potted plant phytometry. Environ.

1003   Monit. Assess. 186, 5041–5057. doi:10.1007/s10661-014-3758-x

1004   Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges

1005   in solitary bees: only few individuals have the capability to cover long foraging distances. Biol.

1006   Conserv. 143, 669–676. doi:10.1016/J.BIOCON.2009.12.003

Figures
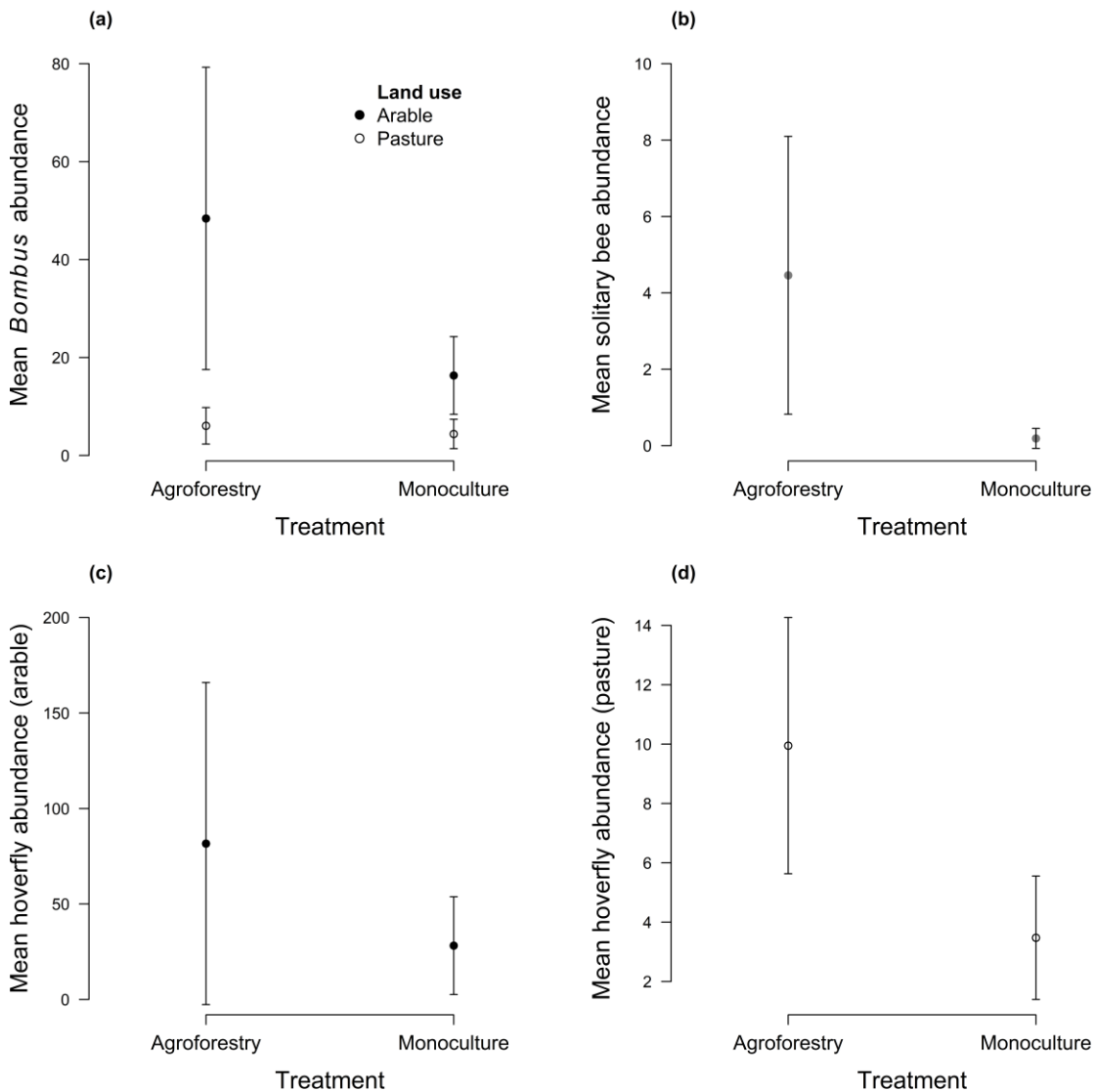
Figure 1 Abundance of wild pollinating insects from transect data. ● = arable land; ○ = pastureland; ◐ = both
land use types. **(a)** Mean bumblebee abundance and 95% CIs; **(b)** Mean solitary bee abundance and 95% CIs;
(c) and **(d)** hoverfly abundance was much higher in arable than pasture systems and these are therefore shown
separately: **(c)** mean hoverfly abundance and 95% CIs, arable systems (figure shows mean abundance across
both arable sites, hence the overlapping confidence intervals; however, model output shows strong evidence
of a treatment effect in arable systems); **(d)** mean hoverfly abundance and 95% CIs, pasture systems.
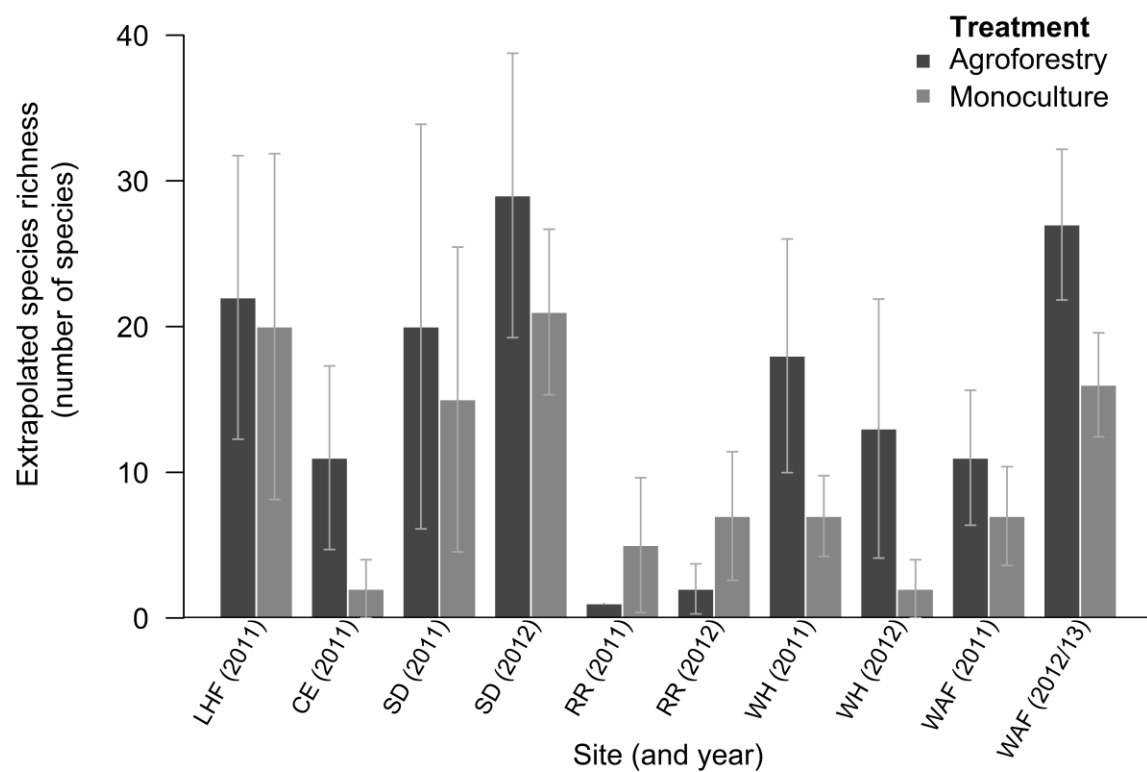
1017

1018   **Figure 2** Species richness (extrapolated to 14 samples) of solitary bees at each site. Bars show 95% confidence

1019   intervals. For site details see Table A.1.
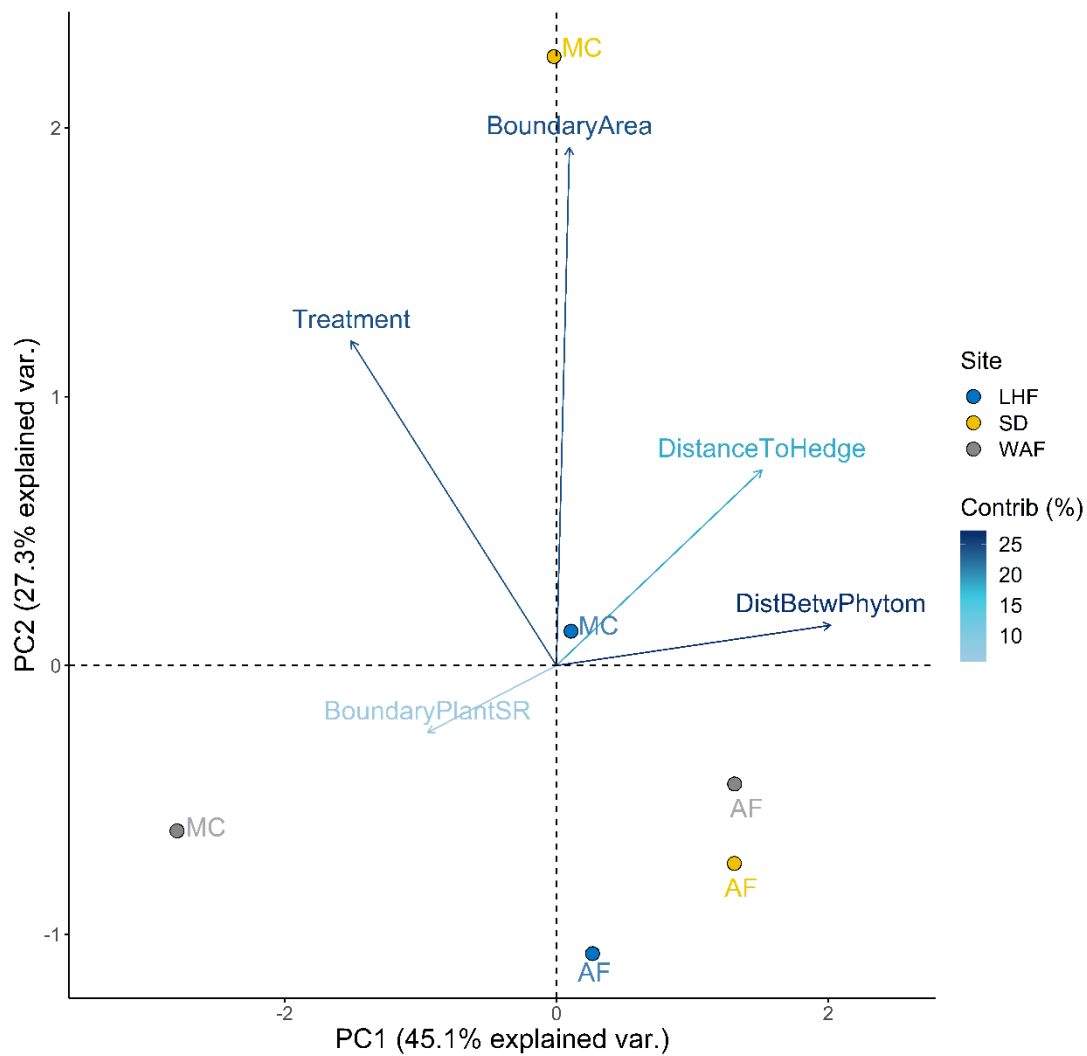
1020

Figure 3 PCA loading plot of 2013 phytometer data. Variables are coloured according to their total contribution (%) to PC1

and PC2 combined. Variable names as follows: tmt, treatment; bound.area = total uncropped area (i.e. hedgerows, field

margins) around field; hedg.dist = distance from the transect to the nearest boundary hedgerow; distbetw = the shortest

(diagonal) distance between phytometer plants; ipBSR = species richness of insect-pollinated plants in field boundary.

Tables

Table 1 ABUNDANCE. Model-averaged parameter estimates from models relating wild pollinating insect abundance to environmental variables. For each pollinator group, regression coefficients (β, standardized at SD = 0.5) are averages of $β_i$ across all models in the top model set, weighted by the Akaike weight w_i of each model in the top model set (Burnham and Anderson, 2002). w_i best = Akaike weight of the best model from each top model subset. Calculations for β only include $β_i$ from models in which a given parameter appears (natural average method). Values in brackets are 95% confidence intervals. Relative variable importance (w_{ip}) is the sum of w_i across all models including that variable (Burnham & Anderson 2002). Variables with the greatest importance for each pollinator group have w_{ip} in bold. NA indicates that the corresponding parameter was not included in any of the top models for that pollinator group. For details of all models in each top model set, see Appendix B.

	Model averaged values					
	Bumblebee abundance◇		Solitary bee abundance◇		Hoverfly abundance◇	
w_i best:	0.45		0.58		0.49	
Parameter*	β	w_{ip}	β	w_{ip}	β	w_{ip}
(Intercept)[†]	1.9522 (1.415, 2.489)		0.3919 (0.161, 0.622)		2.6476 (1.882, 3.413)	
treatment	-0.8861 (-1.323, -0.449)	**1.00**	-1.0427 (-1.380, -0.705)	**1.00**	-1.0648 (-1.833, -0.297)	**1.00**
landuse	-2.0318 (-3.210, -0.854)	**1.00**	-0.1165 (-0.852, 0.619)	0.22	-1.4099 (-2.304, -0.515)	**1.00**
treatment :landuse	1.0529 (0.264, 1.842)	**1.00**	0.5877 (-0.316, 1.492)	0.08	0.5919 (0.306, 0.878)	0.32
sun	-0.5191 (-0.964, -0.074)	0.83	NA	NA	NA	NA
hedg.dist	-0.6943 (-1.250, -0.138)	0.79	-0.8551 (-1.305, -0.405)	**1.00**	NA	NA
bound.area	-0.2389 (-0.732, 0.254)	0.17	0.2164 (-0.171, 0.604)	0.12	-0.2916 (-0.428, -0.155)	0.20
days.sq	NA	NA	-0.1350 (-0.440, 0.170)	0.09	2.2711 (1.188, 3.354)	**1.00**
snh	NA	NA	-0.9477 (-1.458, -0.437)	**1.00**	NA	NA
treatment :snh	NA	NA	1.1564 (0.568, 1.745)	**1.00**	NA	NA

[†] Intercept shows estimated effect when treatment = agroforestry and land use = arable

* Parameters as follows: treatment = agroforestry or monoculture; landuse = land use, arable or pasture; treatment:landuse = interaction between the two previous two parameters; sun = percentage of transect that was sunny; hedg.dist = distance from the transect to the nearest boundary hedgerow; bound.area = total uncropped area (*i.e.* hedgerows, field margins) around field; days.sq = quadratic term, $date^2$, where date is the number of days since 1st March; snh = percentage of semi-natural habitat in 1km buffer round each field; treatment:snh = interaction between treatment and snh. NA values indicate that the variable was not in the model set.

1043 ◊ Bumblebee and hoverfly transect data is from 5 sites in 2011, 4 sites in 2012 and 1 site in 2013 (6 sites across all years);

1044 solitary bee transect data is from 6 sites in 2011, 4 sites in 2012 and 1 site in 2013 (6 sites across all years). See Table A.3

1045 for site-by-year data collection details.

1046

1047

1048 **Table 2** SPECIES RICHNESS. Model-averaged parameter estimates from models relating bumblebee species richness and square

1049 root of solitary bee species richness to environmental variables at six sites. For a full explanation of this table see legend for

1050 Table 1. For details of all models in each top model set, see Appendix B.

	Model averaged values				
	Bumblebee species richness◊		Solitary bee species richness◊		
w_i best:	0.35		0.30		
Parameter*	β	w_{ip}	β	w_{ip}	
(Intercept)†	0.9474 (0.646, 1.249)		3.3742 (2.633, 4.115)		
treatment	NA	NA	-0.6806 (-1.416, 0.055)	0.27	
n.hedg.bound	0.5276 (-0.021, 1.077)	0.51	1.3360 (0.300, 2.372)	0.15	
hedg.dist	NA	NA	1.1926 (-0.081, 2.467)	0.31	
snh	NA	NA	-0.9001 (-2.289, 0.489)	0.13	
bound.area	-0.3945 (-1.069, 0.280)	0.30	NA	NA	

1051 †* Footnotes as for Table 1, with the addition of n.hedg.bound = number of hedged boundaries around field.

1052 ◊ Bumblebee pan trap data is from 5 sites in 2011, 4 sites in 2012 and 1 site in 2013 (6 sites across all years); solitary bee

1053 pan trap data is from 6 sites in 2011, 4 sites in 2012 and 1 site in 2013 (6 sites across all years). See Table A.4 for site-by-

1054 year data collection details.

1055 **Table 3** SEED SET. Model-averaged parameter estimates from models for models relating phytometer seed counts in 2012 to

1056 environmental variables. w_i best = Akaike weight of the best model from the top model subset. For a full explanation of this

1057 table see legend for Table 1. For details of all models in the top model set, see Appendix B.

	Model averaged values	
	Seed count 2012$^\diamond$	
w_i best:	0.68	
Parameter*	β	w_{ip}
(Intercept)†	-0.1088 (-0.666, 0.448)	
treatment	-1.7241 (-2.530, -0.918)	**1.00**
hedg.dist	-1.8241 (-2.908, -0.740)	**1.00**
bound.area	-0.4663 (-1.313, 0.381)	0.32

1058 †* Footnotes as for Tables 1 & 2.

1059 $^\diamond$ Seed count is average number of seeds per fruit. 2012 phytometer data is from 1 pasture and 2 arable sites.

1060   **Table 4** Summary of analyses in which there was strong evidence of a treatment effect.

Taxon or dataset[‡]	Metric	Result[†]	Magnitude of result [Δ]	Land use[*]
Bumblebees	abundance	AF > MC	2.4	a
Hoverflies	abundance	AF > MC	2.0	a, p
Solitary bees	abundance	AF > MC	2.0	a, p
Solitary bees	species richness	AF > MC at 40% of site-by-year samples	10.5	a, p
Solitary bees & plants	species richness correlation	+	NA	a, p
phytometer data, 2012	seed set	AF > MC	4.5	a, p

1061   ‡ All pollinator taxa were sampled in both 2011 and 2012. Plant species richness was sampled in the first year that data

1062   collection was carried out in a field.

1063   † Result shows direction of relationship between AF (agroforestry) and MC (monoculture) treatments, or direction of

1064   correlation (+ = positive).

1065   Δ Magnitude indicates effect size, or how many times higher one value was than the other: *i.e.* bumblebee abundance was

1066   2.4 times higher in AF treatments than MC treatments (in arable land). The value for solitary bee species richness is the

1067   average magnitude across instances where SR was significantly higher.

1068   *Column indicates in which type of land use the result was found: a = arable, p = pasture.