1   **Effects of an agri-environment scheme on bumblebee reproduction at local and**

2   **landscape scales**

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Abstract

Agri-environment schemes (AES) have been implemented across Europe, aiming to mitigate

effects of habitat loss in agro-ecosystems for a range of declining species. These include

pollinating insects such as bumblebees, for which positive effects of AES on abundance and

species richness have been shown. However, there is a lack of evidence for effects of AES

on reproduction of target species, at either local or landscape scales. We conducted a large-

scale study across landscapes exhibiting a gradient of agricultural intensity to investigate the

effects of a targeted flower mixture, sown in patches of three different sizes, on an index of

the total biomass of bumblebee sexuals (males and queens) on replicated transects within

each landscape. We used this index (MQ) as a measure of bumblebee reproduction. After

controlling for floral density on transects, we found that MQ was significantly higher on sown

flower patches than on conventionally managed control patches at local scales throughout

the three-year study. While sown flower patches did not significantly increase MQ in

surrounding landscapes, MQ was higher in landscapes surrounding larger (1 ha) than

smaller (0.25 ha) sown patches. Our results suggest that, while responses of different bee

species may vary depending on the plant species sown, targeted flower mixtures can

enhance bumblebee reproduction by providing locally attractive forage resources to

bumblebees of all castes and sexes from nests within foraging distance. If established at

large enough scales, sown flower patches may lead to a detectable spill-over of

reproductives into surrounding landscapes. Furthermore, effects of sown patches on MQ

were moderated by landscape context, the strongest positive responses being detected at

sites with high proportions of arable land. This supports previous findings that AES can

deliver greater net benefits for pollinators in more intensively farmed landscapes.

Zusammenfassung

Agrar-Umweltprogramme (AES) sind in ganz Europa eingerichtet worden mit dem Ziel, die

Auswirkungen von Habitatverlusten in Agrarökosystemen für eine Reihe von

zurückgehenden Arten zu mildern. Hierzu gehören Bestäuberinsekten wie z.B. Hummeln, für

57 die positive Effekte durch AES auf Abundanz und Artenreichtum gezeigt werden konnten.

58 Indessen mangelt es an Befunden zum Effekt von AES auf die Reproduktion von Zielarten

59 auf der lokalen oder Landschafts-Skala. Wir führten eine großräumige Untersuchung in

60 Landschaften, die einen Gradienten landwirtschaftlicher Intensität darstellten, durch, um den

61 Effekt einer gezielt zusammengestellten Saatmischung, die auf Flächen unterschiedlicher

62 Größe ausgesät wurde, auf einen Index der Gesamtbiomasse der Geschlechstiere von

63 Hummeln (Männchen und Königinnen) zu erkunden, indem wir replizierte Transekte in jeder

64 Landschaft absuchten. Wir benutzten diesen Index (MQ) als ein Maß für die Reproduktion

65 der Hummeln. Nach Kontrolle d er Blütendichte auf den Transekten fanden wir, dass auf der

66 lokalen Skala MQ während der dreijährigen Untersuchungszeit auf den eingesäten

67 Blühflächen signifikant höher war als auf konventionell bewirtschafteten Kontrollflächen.

68 Während eingesäte Blühflächen den MQ-Index in der umgebenden Landschaft nicht

69 signifikant erhöhten, war MQ in Landschaften, die große (1 ha) Blühflächen umgaben, höher

70 als in Landschaften, die kleinere (0.25 ha) Blühflächen umgaben. Unsere Ergebnisse legen

71 nahe, dass, während die Reaktionen unterschiedlicher Bienenarten in Abhängigkeit von den

72 ausgesäten Arten unterschiedlich ausfallen können, zielorientierte Saatmischungen die

73 Reproduktion von Hummeln steigern können, indem allen Kasten und Geschlechtern aus

74 Nestern in Sammelentfernung lokal attraktive Nahrungsressourcen angeboten werden.

75 Wenn sie in ausreichend großem Maßstab eingerichtet werden, können Blühflächen zu

76 einem merklichen spill-over von reproduzierenden Individuen in die um gebende Landschaft

77 führen.

78 Desweiteren wurden die Effekte der Blühflächen auf MQ durch den Landschaftskontext

79 vermittelt, wobei die am stärksten positiven Reaktionen in Landschaften mit hohem Anteil

80 von Agrarflächen gefunden wurden. Dies unterstützt frühere Befunde, nach denen AES den

81 größeren Netto-Nutzen für Bestäuber in intensiver bewirtschafteten Landschaften erbringen

82 kann.

83 **Keywords:** *Bombus,* seed mixture, floral density, pollinators, sexual biomass, foraging,

84 landscape scale

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Introduction

Population declines in many native species within agro-ecosystems have been
attributed partly to the loss and fragmentation of suitable habitats resulting from agricultural
intensification (Tilman, Fargione, Wolff, D'Antonio, Dobson et al. 2001; Winfree, Aguilar,
Vazquez, LeBuhn & Aizen 2009). To mitigate these declines, a number of government-
funded agri-environment schemes (AES) have been implemented (European Economic
Community regulation 2078/92). These compensate farmers for undertaking farming
practices considered favourable to biodiversity, including less intensive management within
cropped areas and creating new habitats on uncropped land. AES have been shown to
benefit birds, bees, butterflies, and plants, leading to increased species richness and
abundance of individuals on focal habitat patches (Carvell, Meek, Pywell, Goulson &
Nowakowski 2007; Pywell, Heard, Bradbury, Hinsley, Nowakowski et al. 2012; Pywell, Meek,
Loxton, Nowakowski, Carvell et al. 2011). However, there has been much debate as to
whether these local-scale benefits translate to effects on long-term declines in farmland
biodiversity (Carvalheiro, Kunin, Keil, Aguirre-Gutiérrez, Ellis et al. 2013; Kleijn & Sutherland
2003). In particular, there is little evidence for positive effects of AES on reproduction and
population persistence of key taxa.

Bumblebees are a group of conservation concern globally, having undergone
widespread declines in range and diversity over recent decades (Cameron, Lozier, Strange,
Koch, Cordes et al. 2011; Williams & Osborne 2009). They are key pollinators of native plant
species and a variety of crops and, together with other wild bees, may provide insurance
against honey bee declines (Garibaldi, Steffan-Dewenter, Winfree, Aizen, Bommarco et al.
2013; Garratt, Coston, Truslove, Lappage, Polce et al. 2014; Winfree, Williams, Dushoff &
Kremen 2007). Bumblebees are eusocial insects with (in temperate regions) an annual
colony cycle. Queens establish colonies in spring and their ability to produce new sexuals
(males and queens) at the end of the cycle is largely dependent on the availability of floral
resources to their worker force within foraging distance of the nest. They therefore require an

113   extensive habitat matrix providing undisturbed nesting sites, accessible foraging resources

114   with a temporal succession of nectar and pollen-rich plants, and mating and hibernation sites

115   (Benton 2006).

116   The importance of food availability for bumblebee reproduction has been inferred

117   from the earlier appearance of queens at flower-rich sites (Bowers 1985). Studies using

118   laboratory-reared colonies placed in the field have shown positive effects of supplementary

119   food (Pelletier & McNeil 2003) or increased floral resources in the landscape on colony

120   growth and numbers of males produced, but mixed effects on queen production, despite

121   positive correlations between worker number and reproductive success (Westphal, Steffan-

122   Dewenter & Tscharntke 2009; Williams, Regetz & Kremen 2012). These studies suggested

123   that spatiotemporal variation in floral resources was a key determinant of reproductive

124   success, and availability of later-season resources could be critical for queen production.

125   Furthermore, bumblebee declines across Europe, particularly in late-emerging species, have

126   been linked to the loss of preferred forage resources such as late-season red clover

127   (*Trifolium pratense*), as a result of agricultural intensification (Bommarco, Lundin, Smith &

128   Rundlöf 2012; Carvell, Roy, Smart, Pywell, Preston et al. 2006; Fitzpatrick, Murray, Paxton,

129   Breen, Cotton et al. 2007; Kleijn & Raemakers 2008).

130   Production of sexuals may therefore be increased in many wild bee species by an

131   increase in food resources available to the provisioning adults. However, since the work of

132   Bowers (1985), few field studies of wild bumblebees have reported counts of sexuals, as

133   opposed to workers. Lye et al. (Lye, Park, Osborne, Holland & Goulson 2009) investigated

134   the effects of habitat management under the Scottish agri-environment scheme on nest-site

135   searching queens during the period of emergence and colony foundation. Rundlöf, Persson,

136   Smith and Bommarco (2014) found higher queen densities in established late-season red

137   clover fields ranging from 4-16 ha than in linear field borders in surrounding landscapes

138   during a single year (Rundlöf, Persson, Smith & Bommarco 2014). Densities of sexuals were

139   also higher in landscapes with, compared to landscapes without, clover fields. However, we

140   know of no studies that have assessed the effects of newly-sown flower mixtures, and the

141   scale of their establishment, on bumblebee reproduction across multiple years, as

142   measured by the abundance of males and queens from wild nests throughout the season.

143   We previously described the response of foraging worker bumblebees to a mixture of

144   nectar and pollen-rich plants sown in experimental patches of different sizes across a

145   gradient of agricultural landscapes (Carvell, Osborne, Bourke, Freeman, Pywell et al. 2011;

146   Heard, Carvell, Carreck, Rothery, Osborne et al. 2007). The mixture was targeted at bees

147   and other pollinators under the Entry Level Stewardship scheme in England (Natural

148   England 2010), aiming to provide floral resources from May to early September, essentially

149   to provision populations during and beyond the main periods of flowering crop bloom. Sown

150   patches attracted higher densities of workers than unsown controls, with this response being

151   strongest in the more intensively farmed landscapes (Carvell et al., 2011). Furthermore,

152   estimates of the number of colonies represented by these foraging workers using molecular

153   genetic methods over a period of three years suggested that, in two species, population

154   growth rates were positive and higher on sown flower patches relative to control habitats in

155   more intensively farmed landscapes (Heard et al. unpublished).

156   Here we present data derived from counts of males and queens from across 28 of

157   the sown and control experimental patches in Carvell et al. (2011) and from conventionally

158   managed field margins in surrounding landscapes. This approach allows us to test whether

159   sown flower patches lead to detectable increases in counts of sexuals in semi-natural

160   habitats in landscapes surrounding the patches, often referred to as a 'spill-over' effect

161   (Hanley, Franco, Dean, Franklin, Harris et al. 2011). Our counts are expressed as an index

162   of the total biomass of bumblebee sexuals, which reflects levels of reproduction or

163   productivity across the different study landscapes, under the assumption that the sexuals

164   observed were most likely to be foraging about a kilometre from their natal nests rather than

165   responding to forage from many kilometres away as part of a dispersal process.

166   We tested the following hypotheses: 1) sown flower patches will enhance total sexual

167   biomass of bumblebees at local and landscape scales; 2) the size of sown flower patches

168   will influence sexual biomass, such that higher densities of males and queens will be

169   recorded on, and in the landscapes surrounding, larger patches; and 3) the effect of sown

170   flower patches on total sexual biomass will vary depending on landscape context, with the

171   strongest positive responses being detected in more intensively farmed areas.

172

173   **Materials and methods**

174   *Experimental design*

175   We selected seven sites across central and eastern England, located between

176   1°40'W and 1°02'E longitude and between 51°10' and 52°56'N latitude, that represented

177   typical land use for their locations but varied widely in landscape characteristics (Appendix

178   A: Table 1). At each site, three patches of different sizes (0.25 ha, 0.5 ha and 1.0 ha) were

179   sown with a mixture of 20% legumes (*Trifolium pratense* of early- and late-flowering

180   varieties, *Trifolium hybridum* and *Lotus corniculatus*) and 80% fine-leaved grasses (*Festuca*

181   *rubra, Poa pratensis* and *Cynosurus cristatus*) (henceforth 'sown patches') as recommended

182   under the AES 'nectar flower mixture' option at the time (Natural England 2010) (seed

183   mixture details given in Appendix A: Table 2). Patches were established on land taken out of

184   arable production (or grass production in one case), typically within a 6 – 30 metre wide strip

185   or block along an existing field edge or corner with crop management continuing across the

186   remainder of the field. We also selected a control patch at each site within conventionally

187   managed non-crop vegetation that was typical for the site and covered at least 0.25 ha. The

188   four patches at a site were separated by an average of 3 km to minimize the influence of

189   bumblebees flying between them (Carvell, Jordan, Bourke, Pickles, Redhead et al. 2012;

190   Knight, Martin, Bishop, Osborne, Hale et al. 2005).

191   Sown patches were established in September 2003 (Carvell et al., 2011). They were

192   subsequently cut twice during the first year (2004) in April and September and thereafter

193   once in September each year to achieve consistent flowering from the perennial legumes

194   and limit domination by unsown weedy species throughout the experiment. However by the

195   summer of 2006, the sown grass species had begun to dominate and reduce cover of the

196   sown legume species so patches were re-sown to maintain floral resource levels for

197 pollinators throughout the experiment. This was performed in September 2006 with a mixture

198 of the same legume species as previously used that excluded grasses. In addition a small

199 amount of the annual *Centaurea cyanus* (2%) was added to the mixture to help ensure

200 flowering in the first year (Appendix A: Table 2).

201   To assess densities of males and queens on patches, two 2 m x 100 m transects

202 were established in the centre of each sown and control patch, with a minimum of 6 metres

203 separating them (hereafter 'local' transects). To assess the effect of sown flower patches on

204 male and queen densities in the landscapes surrounding each patch (i.e. to quantify 'spill-

205 over' effects), four 2 m x 100 m transects were established at random in conventionally

206 managed field margins within 1000 m of the centre of each patch (hereafter 'landscape'

207 transects). Straight-line distances between the centre of each landscape transect and the

208 corresponding sown or control patch were on average 371 m (SE ± 48 m), and did not differ

209 significantly between sites (ANOVA F = 1.73, df = 6, P = 0.12) or between patches within

210 sites (ANOVA F = 0.56, df = 3, P = 0.64). This would have allowed bees from nests located

211 within typical foraging distance of the patch to access both local patch and/or landscape

212 transects at each site. Of the four landscape transects per site, two were located along the

213 margins of arable fields, one along the margin of an improved or semi-natural grassland

214 depending on the landscape, and one along the edge of a woodland in order to fully

215 represent typical vegetation for each site. This gave a total of 24 sampling transects (8 local

216 and 16 landscape transects) per site.

217

218 *Bumblebee and flower surveys*

219   Males and queens of all social *Bombus* species were recorded in monthly surveys

220 from June to September over the three years 2005 – 2007. Queen activity during earlier

221 months (April and May) was not recorded as we considered that these were most likely to be

222 foundress queens rather than newly-emerged queens produced by colonies located within

223 each landscape. On each survey, individuals visiting flowers were counted along all

224 transects and the visited plant species was noted. The order in which the six transects on or

225   surrounding each patch were visited was varied between surveys. Our surveys were

226   conducted within a larger study that included counts of workers (Carvell et al. 2011) for

227   which the ecologically similar species *Bombus terrestris* and *B. lucorum* were recorded as a

228   group, denoted *B. terrestris* agg., as their workers cannot be distinguished reliably in the

229   field. For consistency, we recorded males or queens of these two species as *B. terrestris*

230   agg. For *B. ruderatus*, only fully melanic individuals were recorded separately to species

231   level, due to the difficulty of separating banded individuals from *B. hortorum* in the field (Ellis,

232   Knight & Goulson 2005). While melanic individuals could have included some *B. hortorum*,

233   molecular analyses have since shown all such full melanics to have the *B. ruderatus*

234   genotype (Dreier, Redhead, Warren, Bourke, Heard et al. 2014). Transect visits were carried

235   out between 10.00 and 17.30 during dry weather when ambient temperature was above 13

236   °C with at least 60% clear sky, or above 17 °C under any sky conditions, and wind speeds

237   up to 5 on the Beaufort wind scale.

238   To measure floral density on each survey, we identified all flowering dicotyledonous

239   species and scored their flower abundance within ten 2 m × 10 m sections of each transect,

240   within the following ranges: 1–5; 6–25; 26–200; 201–1000; 1001–4999 and 5000+ flower

241   units (defined as a single flower or an umbel, spike or capitulum on multi-flowered stems).

242   Flower abundance was expressed as the mid-point value for each range (with a value of

243   12000 for the 5000+ category), and summed across all ten sections, giving a monthly

244   estimate of the density of flowering units per transect. Subsequently we selected only plant

245   species visited by male or queen bumblebees during the study. The summed flower

246   abundance of these species was used as a measure of floral density.

247

248   *Landscape context*

249   Habitat surveys were undertaken to characterise the landscape surrounding each

250   patch. In July 2004 all land parcels (defined areas of continuous land-use) within 1000 m of

251   the patch centre were visited and categorised according to their broad land-use type and

252   habitat composition. This radius took account of estimates of worker foraging distance for

253   the most frequent *Bombus* species in our study (Knight et al. 2005; Knight, Osborne,

254   Sanderson, Hale, Martin et al. 2009). These data were digitised onto a UK Ordnance

255   Survey base map using Arc GIS software (ESRI), allowing for edits in parcel location, shape,

256   and size. Parcel attributes were then extracted to allow calculation of the total area of each

257   broad land-use type (hereafter 'landscape context') within 1000 m of each patch (Appendix

258   A: Table 1). We used the proportion of arable land (cropped fields) as our key measure of

259   landscape context for analyses (as in Carvell et al. 2011), as this variable was significantly

260   negatively correlated with proportions of improved grassland ($r = -0.84$, $P < 0.001$), built-up

261   areas ($r = -0.37$, $P = 0.03$) and semi-natural habitats ($r = -0.66$, $P < 0.001$).

262

263   *Statistical analysis*

264   All analyses were carried out in R (version 2.8.1). Of a potential total of 672 bee

265   surveys over three years, 8 were missed on the experimental patches due to cutting or re-

266   sowing in early September before the sampling visit and were identified as missing values in

267   all analyses.

268

269   *Calculating an index of total sexual biomass combining male and queen counts (MQ)*

270   We used an index of sexual biomass (MQ) that combines counts of males and

271   queens as follows: 'MQ' = M + 3Q, where M = number of males and Q = number of queens

272   (Pelletier et al. 2003). This reflects the greater investment of time and resources required to

273   rear queens, on a per capita basis, than males (Beekman & van Stratum 1998; Lopez-

274   Vaamonde, Raine, Koning, Brown, Pereboom et al. 2009). Values of MQ and floral density

275   were calculated for each survey for: i) local transects (total counts across two control or

276   sown transects) and ii) landscape transects (total counts across four conventionally

277   managed field margin transects in landscapes surrounding each patch). The three most

278   abundant *Bombus* species were analysed separately, with counts of the less abundant

279   species included in the summed MQ for all species, designated 'total *Bombus*'.

280

281 *Effects of sown flower patches at local and landscape scales*

282   We used Generalized Linear Models to assess the effect of sown flower patches on

283 MQ, with separate analyses of the data from local and landscape transects in order to

284 compare habitats at equivalent scales both within and between study sites. Analysis began

285 with a maximal model that included patch type (sown *vs.* control), site and year as fixed

286 effects, and a two-way interaction of patch type with year to account for possible temporal

287 variation. Floral density of visited plants was added as a covariate to account for variation

288 due to differences in flower abundance over time and between patches. Models were fitted

289 assuming a Poisson distribution with a log-link function, and an offset for the number of

290 transects per survey. An adjustment for overdispersion was added in cases where the

291 Pearson Chi-squared statistic exceeded its associated degrees of freedom by more than

292 two-fold. Thereafter, we applied a series of likelihood ratio tests in order to remove terms

293 sequentially from the maximal model until only significant interactions and main effects ($P <$

294 0.05) remained (Crawley 2005).

295

296 *Effects of patch size*

297   To test whether the size of the three sown flower patches had an effect on MQ, we

298 fitted additional models in which patch size (0.25 ha, 0.5 ha, 1.0 ha) replaced the binary

299 patch type classification within the minimal adequate model. Each patch size model was

300 tested against the equivalent model with identical effects at all sown patches using likelihood

301 ratio tests to produce an F statistic to assess the significance of the difference between the

302 two models. A statistically significant deterioration in fit therefore implies a difference

303 between the effects of patches of different sizes.

304

305 *Effects of landscape context*

306   Effects of landscape context on the response of MQ to sown flower patches were

307 tested using linear models with normally-distributed errors and a log-link function. Means of

308 predicted values from the minimal adequate models with patch type were used in cases

309 where patch size was not significant, and means from the models with patch size were used

310 where this term was significant. There were no significant interactions between year and

311 patch type in the models described (aside from one case for *B. terrestris*). Predicted values

312 of MQ were therefore averaged across years, before the fitting of separate regressions of

313 mean MQ per 100 m transect from control and sown flower patches against the proportion of

314 arable land in the surrounding landscape.

315

316 **Results**

317 Across all transect counts, we recorded a total of 1306 males and 203 queens (in 2005: 565

318 males and 107 queens; in 2006: 275 males and 25 queens; in 2007: 466 males and 71

319 queens). These represented nine social bumblebee species (details given in Appendix A:

320 Table 4). The most abundant were *Bombus lapidarius*, *B. pascuorum* and *B. terrestris* agg.,

321 accounting for 53%, 15% and 20% of all observations, respectively. Males and queens were

322 observed visiting 53 different flowering plant species. The legume species *T. pratense, T.*

323 *hybridum* and *L. corniculatus* sown on the experimental patches together accounted for 21%

324 of all flower visits by males and 53% of all visits by queens. Species receiving a high

325 proportion of visits on transects in the surrounding landscapes were, in descending order, for

326 males, *Cirsium vulgare, Picris echioides, Senecio jacobaea, Cirsium arvense* and *Centaurea*

327 *nigra* (together accounting for 57% of visits) and, for queens, *Cirsium vulgare, Ballota nigra*

328 and *Lamium album* (together accounting for 26% of visits). Analyses comparing floral density

329 on sown and control patches, between sites and across years are presented in Carvell et al.

330 (2011). These showed no difference between sites or sown patches within sites in each

331 year, but significantly higher floral density on sown patches than controls in each year, and

332 significant variation between years, with highest floral density on sown patches in 2005,

333 decreasing in 2006 and increasing again in 2007 (Carvell et al., 2011). Full lists of plant

334 species constituting >1% of all flower counts on both the local patch transects and

335 landscape transects are given in Appendix A: Table 3.

336

337 *Effects of sown flower patches at local and landscape scales*

338 Floral density was a significant predictor of MQ at both local and landscape scales for all

339 species except *B. pascuorum* (Table 1). We therefore present the means (MQ per 100 m

340 transect) of fitted values from the minimal adequate models for each species or group in

341 order to demonstrate differences between sown and control patches over and above the

342 influence of floral density. Study site was a significant factor in the models for 'total *Bombus*',

343 *B. lapidarius* and *B. pascuorum* on both local and landscape transects, and this effect is

344 explored further in the regression analysis of MQ against landscape context.

345 On the local transects, MQ for 'total *Bombus*', *B. lapidarius* and *B. pascuorum* was

346 significantly higher on sown flower patches than on conventionally managed control patches

347 in all three years of the study (Table 1A; Fig. 1). For *B. terrestris* agg. on local transects, the

348 effect of patch type was non-significant. Significant differences between years were detected

349 for all species (Table 1A), with a tendency for lower counts in 2006 than in 2005 or 2007, but

350 with *B. pascuorum* showing a significant increase in mean MQ per transect per year from

351 0.11 to 0.56 over the three years.

352 We did not find higher MQ on landscape transects surrounding sown patches than on

353 transects surrounding unsown controls (Table 1B, Fig. 2), even though total sexual biomass

354 was highest overall in landscape sectors containing a sown patch (considering both local

355 and landscape transects together). On the landscape transects, MQ was nearly five times

356 lower than on local transects on the sown patches (ratio of mean MQ per transect for total

357 *Bombus* on sown local: landscape transects = 2.4:0.5), and was roughly equal to MQ on

358 local transects on the control patches (ratio=0.6:0.5). Effects of patch type on MQ on the

359 landscape transects were non-significant for total *Bombus* and *B. pascuorum*. For *B.*

360 *lapidarius*, MQ was significantly lower on landscape transects surrounding sown flower

361 patches than on landscape transects surrounding control patches (Table 1B). Significant

362 differences between years were detected for each species (but not the 'total *Bombus*'

363 group), and for *B. terrestris* the effect of patch type depended on year (significant year x

364 patch type interaction, Table 1B), with lower MQ on landscape transects surrounding sown

365   patches (relative to control patches) in 2005 and 2007. Our first hypothesis (that sown flower

366   patches will enhance total sexual biomass of bumblebees at local and landscape scales) is

367   therefore supported at local scales but not at landscape scales when looking in isolation at

368   MQ on landscape transects surrounding the focal patches.

369

370   *Effects of patch size*

371   At the local scale, the size of sown flower patches did not have a significant effect on MQ for

372   any species (Table 1A). However, significant effects of patch size were found at the

373   landscape scale (Table 1B, Fig. 2). MQ was highest on transects in landscapes surrounding

374   the largest sown flower patches (covering 1 ha) for the 'total *Bombus*' group and *B.*

375   *lapidarius*. The effect of patch size was also significant for *B. pascuorum*, with higher MQ on

376   landscape transects surrounding sown 0.5 ha patches than on those surrounding 0.25 ha or

377   1 ha patches (Fig. 2). Our second hypothesis (that the size of sown flower patches will

378   influence sexual biomass, such that higher densities of males and queens will be recorded

379   on, and in the landscapes surrounding, larger patches) is therefore supported at the

380   landscape scale for some species but not at local scales.

381

382   *Effects of landscape context*

383   For the control patches, there were no significant relationships between MQ and the

384   proportion of arable land at either local or landscape scales (Table 2). For sown flower

385   patches, there was a significant positive relationship between the proportion of arable land

386   and MQ for 'total *Bombus'* and *B. terrestris* agg. and a marginally non-significant positive

387   relationship for *B. lapidarius* (P = 0.07) at the local scale. In other words, there was higher

388   sexual biomass on sown patches than on control patches in the most intensively farmed

389   landscapes, but sexual biomasses on sown and control patches were similar in less

390   intensively farmed landscapes (Figs 3A -D).

391   On the landscape transects surrounding sown patches, there were significant positive

392   relationships between MQ and proportion of arable land for 'total *Bombus*' and *B. lapidarius*

(Table 2). Higher numbers of sexuals were recorded in the more intensively farmed landscapes, but only on landscape transects associated with the largest sown patches (1 ha) was MQ higher than on transects associated with control patches (Fig. 4). Effects on MQ of the proportion of arable land for *B. pascuorum* were non-significant, though numbers of *B. pascuorum* sexuals were low (Appendix A: Table 2), and, in contrast to the other species, showed a trend for a negative relationship (Fig. 4C). Our third hypothesis (that the effect of sown flower patches on total sexual biomass will vary depending on landscape context) is therefore supported for some species.

Discussion

We compared standardised counts of bumblebee sexuals visiting transects on sown patches of flowers and in the landscapes surrounding sown patches, with counts of sexuals visiting transects on or surrounding unsown, control patches. These counts were expressed as an index of total sexual biomass (MQ) to reflect the greater investment of time and resources required to rear queens relative to males. Sown patches providing high densities of floral resources throughout the season significantly enhanced MQ at local (patch) scales. This effect was consistent over three years. At landscape scales, overall effects of sown flower patches were not detected when comparing MQ on transects surrounding them with MQ on transects surrounding unsown patches. However, the size of sown patches did influence sexual biomass at landscape scales, with higher densities of males and queens being recorded in landscapes surrounding larger sown patches of 1 ha or 0.5 ha depending on species. We also found that for the dominant species, *Bombus lapidarius*, and summed 'total *Bombus'*, effects of sown patches on total sexual biomass were moderated by landscape context. The strongest positive responses were detected at sites with high proportions of arable land (as found for worker bumblebees (Carvell et al. 2011)).

Our results may have been influenced by one species in particular, *Bombus lapidarius*, which is common across much of NW Europe and accounted for 53% of all counts.

421 Nevertheless, we present significant patterns for two other widespread and common species

422 and include an additional six species in a summed MQ index representing 'total *Bombus*'.

423 The question of whether the sown flower patches enhanced reproduction within local

424 bumblebee populations or attracted sexuals in from many kilometres away (particularly in the

425 highly arable landscapes) is central to the interpretation of these results. Here we consider

426 flower preferences, flight distances and colony dynamics to offer possible explanations.

427

428 The legume (Fabaceae) species sown in our study represent highly rewarding nectar and

429 pollen resources for worker bumblebees from May to late August (Carvell et al. 2011; Pywell,

430 Warman, Hulmes, Hulmes, Nuttall et al. 2006), hence are likely to have enhanced colony

431 growth and potentially enhanced reproductive success of nests within foraging distance

432 (Williams et al. 2012). The flower preferences of males and queens differ from those of

433 workers and from each other (Benton 2006). For example, *B. lapidarius* males favour

434 *Cirsium vulgare* and other open flowers for nectar collection but have no requirement for

435 pollen, whereas newly-emerged queens favour *Trifolium pratense* and other long-corolla

436 flowers from which they consume large amounts of pollen (Carvell et al. 2007). Both types of

437 flower were available to sexuals in our study, and, as expected, floral density on transects

438 was a significant predictor of sexual biomass for *B. lapidarius* and *B. terrestris*. In addition to

439 containing attractive forage plants most sown patches were grassy and linear in shape,

440 offering males good opportunities for patrolling for mates. This may explain why we found

441 higher sexual biomass (dominated by male densities) on sown patches than on controls or

442 surrounding landscape transects, in contrast to a previous study that found higher male

443 densities on landscape transects than on pure clover fields (Rundlöf et al. 2014).

444

445 Floral density (of plant species visited by all *Bombus* species) did not relate to sexual

446 biomass of *B. pascuorum*, and this may have been due to the more specialised flower

447 choices of the species. For example, throughout the study *B. pascuorum* males were

448 recorded visiting 15 plant species whereas *B. lapidarius* males were recorded visiting a total

449   of 34 species. Nevertheless, MQ was consistently greater on sown flower patches than on

450   control patches at the local scale, over and above the influence of floral density, suggesting

451   that sown patches enhanced reproduction in local populations of the three focal species.

452

453   With regard to flight distances and the scale at which sown flower patches affect the

454   distribution of males and queens, our data suggest that sown patches may attract sexuals

455   over a short range from the surrounding landscape, if those sexuals travel over distances

456   similar to the foraging distance of workers (estimated in the region of 200 – 1000 m in UK

457   landscapes similar to those surveyed here (Carvell et al. 2012; Knight et al. 2005)). For

458   patches of 0.25 ha or 0.5 ha, we found lower sexual biomass on the landscape transects

459   within 1 km of sown patches than on the landscape transects surrounding control patches

460   (for *B. lapidarius* in all years, and *B. terrestris* in 2007). This could have occurred if the

461   majority of sexuals in landscapes with sown patches were being drawn into them to forage,

462   and if, in landscapes with no sown patch, sexuals were more evenly distributed. Where

463   larger patches of 1 ha were sown, local MQ did not differ from that on smaller patches

464   suggesting that overall numbers of sexuals were higher on larger patches. Larger patches

465   may also have been more easily detectable and attracted more foragers as a result.

466   Furthermore, sexual biomass on the landscape transects surrounding larger patches was

467   equal to or higher than that on those surrounding control patches, suggesting a weak spill-

468   over effect from sown patches into surrounding semi-natural habitats (Hanley et al. 2011).

469   We cannot rule out longer-range attraction to sown resources since flight distances of newly-

470   emerged males and queens may exceed those of workers. While evidence is limited, male

471   and queen dispersal have been estimated at several kilometres (Dreier et al. 2014; Kraus,

472   Wolf & Moritz 2009; Lepais, Darvill, O'Connor, Osborne, Sanderson et al. 2010), though

473   newly-emerged queens are known to return to their natal colonies to shelter and build

474   reserves for the winter. Attraction of sexuals at large spatial scales could still constitute a

475   beneficial effect on local populations if sown flower patches enhanced male and queen

476 fitness, mating or hibernation opportunities through the provision of additional foraging and

477 other habitats.

478

479 We found the strongest effects in the most arable landscapes with a lack of alternative

480 forage resources (Figs. 3 and 4), consistent with similar analyses on abundances of worker

481 bumblebees and other pollinators (Carvell et al. 2011; Scheper, Holzschuh, Kuussaari,

482 Potts, Rundlöf et al. 2013). It is likely that the detection probability for males and queens on

483 semi-natural habitats is greater in more arable landscapes due to increased aggregation or

484 attraction to floral resources where overall cover of foraging habitats is low (Scheper et al.

485 2013). In addition, we might expect the spill-over effect from sown flower patches to increase

486 in landscapes where a higher proportion of colonies were foraging on them, as seems

487 plausible in the intensive arable landscapes here. These patterns were not shown by *B.*

488 *pascuorum* for which a non-significant negative relationship was found between sexual

489 biomass and proportion of arable land at the landscape scale. This may reflect the close

490 association of *B. pascuorum* with grassland habitats for nesting and foraging; so

491 *B.pascuorum* reproduction in predominantly arable landscapes may be limited not only by

492 forage, but by above-ground nest site availability and nest-forage configuration; thus

493 highlighting the value of existing semi-natural habitats in more complex landscapes

494 (Goulson, Lepais, O'Connor, Osborne, Sanderson et al. 2010; Kennedy, Lonsdorf, Neel,

495 Williams, Ricketts et al. 2013). The reasons for the differential landscape-scale effect of

496 sown patch size on *B. pascuorum* (highest MQ on 0.5 ha patches) to *B. lapidarius* and 'total

497 *Bombus*' (highest MQ on 1.0 ha patches) are more difficult to determine. Numbers of *B.*

498 *pascuorum* were low on landscape transects (52 sexuals, Appendix A: Table 4), suggesting

499 that with analysis based at the patch level, these low numbers may have influenced our

500 results.

501

502 Considering colony dynamics, reproductive success in bumblebees can be highly variable

503 between colonies. In studies using captive-reared *B. terrestris* colonies, most or all produced

504 males but only between 15-50% produced queens (Lopez-Vaamonde et al. 2009; Westphal

505 et al. 2009). Wild colonies may experience even lower rates of queen production, though

506 studies that directly measure counts of known offspring from wild nests are extremely rare

507 (Cumber 1953) . Furthermore, consistent with our data, numerical sex ratios in bumblebees

508 tend to be highly male-biased (in *B. terrestris* reared in semi-natural conditions, the

509 numerical sex ratio was c. 50 males: 1 queen (Lopez-Vaamonde et al. 2009)). Thus higher

510 densities of males in a particular landscape act as an indicator of the potential for population

511 growth, but only indirectly. Numbers of sexuals were not reduced during 2006 and 2007 to

512 the same extent as numbers of workers of the same species, which may have suffered from

513 poor weather and reduced flowering from the sown flower patches (Carvell et al. 2011).

514 Furthermore, *B. pascuorum* showed a trend for increasing total sexual biomass over time, as

515 would be predicted from our finding of positive population growth rates on sown patches

516 (Heard et al. unpublished). Studies on the effects of landscape-level resources at the colony

517 level are emerging from the application of molecular genetic methods (Carvell et al. 2012),

518 but there is still a need for better understanding of the dynamics of different castes in wild

519 bumblebee populations.

520

521 *Conclusions*

522 Our study provides important evidence for effects of landscape-level enhancements via a

523 targeted agri-environment scheme on bumblebee reproduction as measured by the

524 abundance of males and queens from wild nests. It suggests that sown flower mixtures

525 providing season-long resources can enhance reproduction via an increase in the production

526 of sexuals from nests within foraging distance. If sown patches are established at large

527 enough scales (of at least 1 ha), this response may lead to spill-over effects into surrounding

528 semi-natural habitats, particularly in intensively farmed landscapes. This is consistent with

529 two recent meta-analyses at European (Scheper et al. 2013) and global (Kennedy et al.

530 2013) scales, suggesting that farms within 'simple' or intensified agricultural landscapes

531 receive substantial benefits for pollinators from on-farm diversification. Our study adds to the

532 evidence base for enhancing forage resources in arable landscapes, but this should not

533 detract from the use of flower mixtures where appropriate in more heterogeneous

534 landscapes (including grass-dominated areas) or floral enhancement via other agri-

535 environment measures such as organic farming, to benefit the full pollinator community or

536 species of conservation concern.

537

538 The effectiveness of the 'nectar flower mixture' option under the Entry Level Stewardship

539 (ELS) scheme in England is currently limited by low uptake and variable establishment

540 quality, despite around 60% of England's agricultural land being managed under ELS. For

541 example, although growers are provided with guidance on sowing and management,

542 including that the mixture is sown in patches of up to 1 ha (Natural England, pers. comm.),

543 the total area sown across England (as of January 2013) was around 3,618 ha. This

544 represents only 0.06% of all land covered by ELS and only 6.6% of all ELS agreements

545 (POSTNOTE 2013). Further evidence of the effects of floral enhancements on bumblebee

546 reproduction and other parameters such as foraging distance is required, and could be

547 modelled for different landscapes to inform the spatial location and extent of patch sowing

548 required. Furthermore, the costs of establishing and effectively maintaining agri-environment

549 options may vary depending on the farming system and should be appraised against the

550 likely benefits for pollinator habitat provision and agricultural production more widely

551 (Breeze, Bailey, Balcombe & Potts 2014). The mechanistic relationships between

552 bumblebee distributions, population dynamics and landscape quality are still poorly

553 understood (Williams et al. 2012). Such information is central to understanding population

554 responses to landscape change and mitigation measures, and to predicting the resulting

555 impacts on pollination services.

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566   **Appendix A.** Supplementary data

567   Supplementary data associated with this article can be found in the online version, at

568   XXXXXX.

569

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Figure captions

Fig. 1. Index of bumblebee sexual biomass (MQ, see text), at the local scale on sown flower patches (filled bars) vs control patches (open bars). Results shown are means (per 100 m transect, per survey) of predicted values from minimal adequate models in Table 1A with standard errors calculated from data aggregated at the level used in statistical analyses. The effect of patch type was significant for all species shown ($P<0.01$), and non-significant for *B. terrestris* agg. (not shown).

Fig. 2. Index of bumblebee sexual biomass (MQ, see text), at the landscape scale on conventionally managed margins of fields surrounding sown flower patches of different sizes (0.25 ha, 0.5 ha, 1 ha) and unsown controls. Results shown are means (per 100 m transect, per survey) of predicted values from minimal adequate models in Table 1B with standard errors calculated from data aggregated at the level used in statistical analyses. 'Size diff' = significance of differences between the three sown patches of different size; *** $P<0.001$; **$P<0.01$; NS = not significant.

Fig. 3. Relationships between predicted bumblebee sexual biomass (MQ) per 100 m at each site on local transects on sown flower (filled circles) and control (open circles) patches and the proportion of arable land within 1000 m, for (A) total *Bombus*, (B) *Bombus lapidarius*, (C) *Bombus pascuorum* and (D) *Bombus terrestris* agg.. Curves representing sown (solid line) and control (dashed line) patches were fitted using the slope and intercept values from each model (Table 2).

Fig. 4. Relationships between predicted bumblebee sexual biomass (MQ) per 100 m at each site on landscape transects surrounding sown flower patches of different sizes and the proportion of arable land, for (A) total *Bombus*, (B) *Bombus lapidarius*, (C) *Bombus pascuorum* and (D) *Bombus terrestris* agg.. Curves representing different patch sizes were fitted using the slope and intercept values from each model (Table 2).

750   **Table 1.** Model results showing the effects of sown flower patches on total biomass of

751   bumblebee sexuals (MQ) at (A) local and (B) landscape scales. Test statistics at the point of

752   deletion from the model are shown, with terms retained in the minimal adequate model for

753   each species shown in bold. [1]Effects of patch type relate to differences between sown and

754   control patches, with identical effects at all sown patches. [2]Effects of patch size relate to

755   differences between the three sown patches of different size (0.25 ha, 0.5 ha and 1 ha).

756   [3]Floral density was positively related to MQ in cases where the term was significant. Main

757   effects included in significant interactions are not given separate test statistics.

758   **(A)**

Model terms	df	Total *Bombus* F	P	*B. lapidarius* F	P	*B. pascuorum* F	P	*B. terrestris* agg. F	P
Patch type[1]	1	11.474	**0.001**	11.432	**0.001**	6.971	**0.009**	3.061	0.081
Site	6	4.356	**0.000**	4.748	**0.000**	3.733	**0.001**	1.977	0.069
Year	2	5.718	**0.004**	4.054	**0.018**	13.565	**0.000**	4.962	**0.008**
Floral density[3]	1	9.169	**0.003**	7.179	**0.008**	0.600	0.439	18.375	**0.000**
Y x P type	2	0.101	0.904	0.364	0.695	0.685	0.505	1.564	0.211
Patch size[2]	2	0.688	0.503	1.828	0.162	0.084	0.920	0.116	0.890

759   **(B)**

Model terms	df	Total *Bombus* F	P	*B. lapidarius* F	P	*B. pascuorum* F	P	*B. terrestris* agg. F	P
Patch type[1]	1	3.734	0.054	4.023	**0.046**	3.373	0.066		
Site	6	3.144	**0.005**	4.122	**0.001**	20.557	**0.002**	1.879	0.084
Year	2	2.235	0.109	4.069	**0.018**	8.445	**0.015**		
Floral density[3]	1	15.087	**0.000+**	5.303	**0.022**	1.836	0.175	6.836	**0.009**
Y x P type	2	2.128	0.121	1.105	0.333	3.086	0.214	3.203	**0.042**
Patch size[2]	2	5.649	**0.004**	8.158	**0.000**	21.224	**0.000**	0.554	0.767

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Table 2. Regression statistics for linear models relating total biomass of bumblebee sexuals

(MQ) to the proportion of arable land within 1000 m of each patch.

Transect type			Total Bombus	B. lapidarius	B. pascuorum	B. terrestris agg.
Local (on patches)	Sown (mean all sizes)	R^2	0.610	0.511	0.037	0.651
		slope	0.031	0.037	0.006	0.009
		P	**0.038**	0.071	0.678	**0.028**
	Control	R^2	0.564	0.479	0.037	0.034
		slope	0.026	0.032	0.006	0.000
		P	0.052	0.085	0.678	0.694
Landscape (conventional margins)	Sown (1ha)	R^2	0.575	0.715	0.033	0.138
		slope	0.033	0.044	0.005	0.008
		P	**0.048**	**0.017**	0.698	0.412
	Sown (0.5ha)	R^2	0.508	0.786	0.495	0.337
		slope	0.027	0.053	-0.022	-0.001
		P	0.072	**0.008**	0.078	0.172
	Sown (0.25ha)	R^2	0.642	0.538	0.154	0.016
		slope	0.017	0.023	-0.009	0.000
		P	**0.030**	**0.061**	0.384	0.787
	Control	R^2	0.297	0.430	0.221	0.103
		slope	0.013	0.026	-0.011	0.000
		P	0.206	0.110	0.287	0.483

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Fig. 1
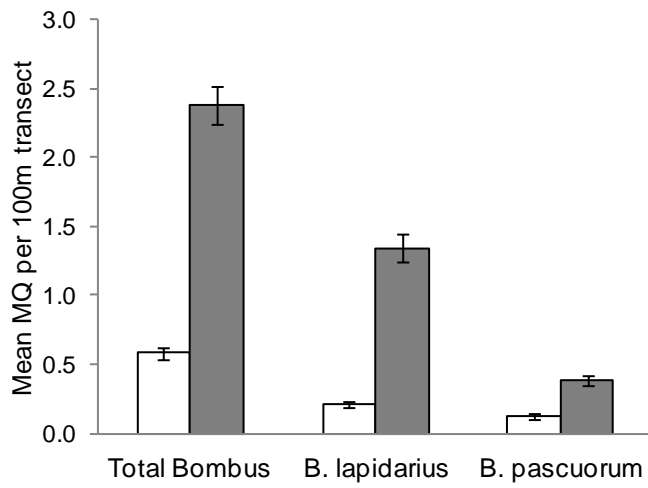
Fig. 2.

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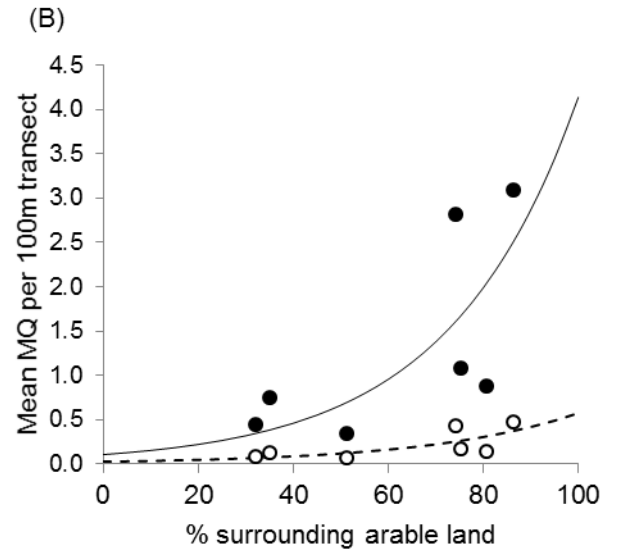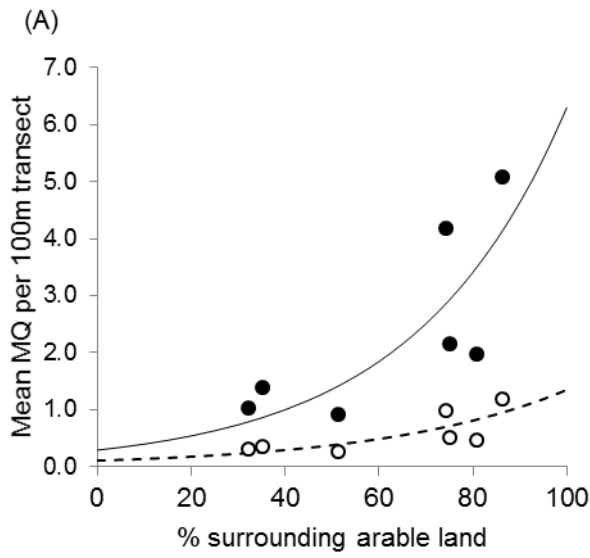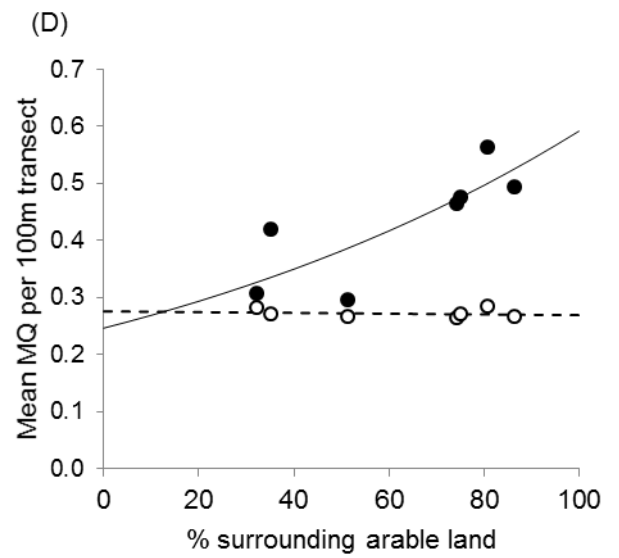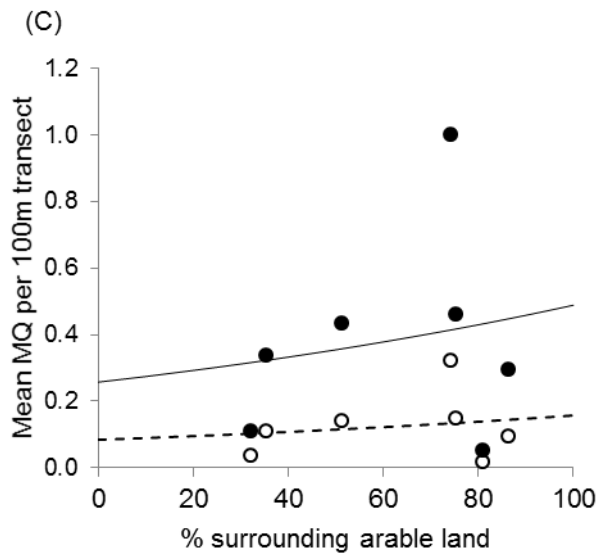
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Fig. 3.

(A)

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(C)

(B)

(D)
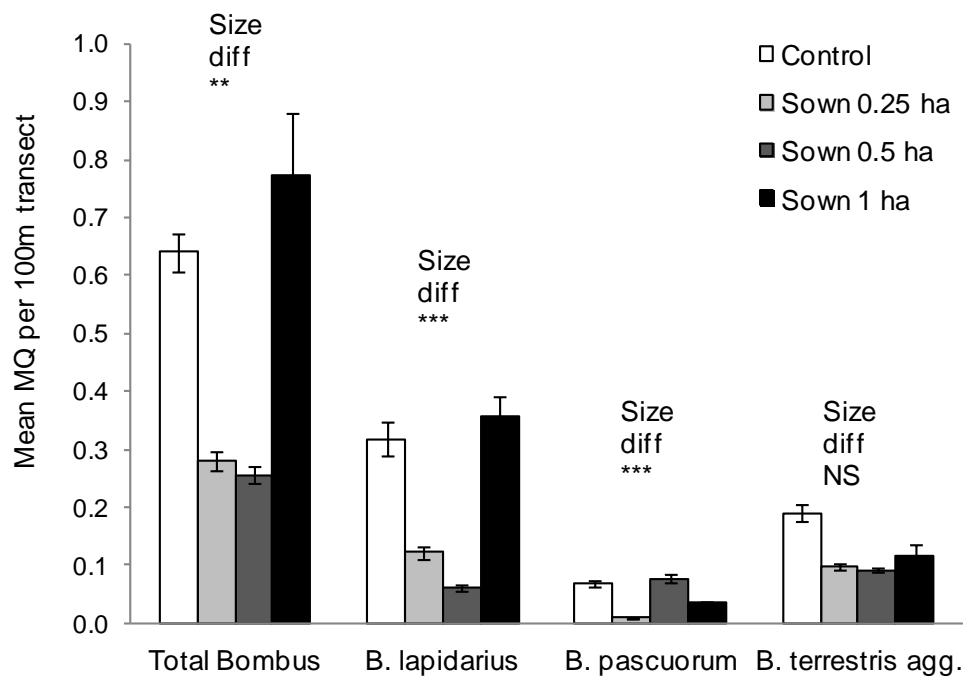
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Fig. 4