

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

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29 **Abstract**

30 Agri-environment schemes (AES) have been implemented across Europe, aiming to mitigate
31 effects of habitat loss in agro-ecosystems for a range of declining species. These include
32 pollinating insects such as bumblebees, for which positive effects of AES on abundance and
33 species richness have been shown. However, there is a lack of evidence for effects of AES
34 on reproduction of target species, at either local or landscape scales. We conducted a large-
35 scale study across landscapes exhibiting a gradient of agricultural intensity to investigate the
36 effects of a targeted flower mixture, sown in patches of three different sizes, on an index of
37 the total biomass of bumblebee sexuals (males and queens) on replicated transects within
38 each landscape. We used this index (MQ) as a measure of bumblebee reproduction. After
39 controlling for floral density on transects, we found that MQ was significantly higher on sown
40 flower patches than on conventionally managed control patches at local scales throughout
41 the three-year study. While sown flower patches did not significantly increase MQ in
42 surrounding landscapes, MQ was higher in landscapes surrounding larger (1 ha) than
43 smaller (0.25 ha) sown patches. Our results suggest that, while responses of different bee
44 species may vary depending on the plant species sown, targeted flower mixtures can
45 enhance bumblebee reproduction by providing locally attractive forage resources to
46 bumblebees of all castes and sexes from nests within foraging distance. If established at
47 large enough scales, sown flower patches may lead to a detectable spill-over of
48 reproductives into surrounding landscapes. Furthermore, effects of sown patches on MQ
49 were moderated by landscape context, the strongest positive responses being detected at
50 sites with high proportions of arable land. This supports previous findings that AES can
51 deliver greater net benefits for pollinators in more intensively farmed landscapes.

52

53 **Zusammenfassung**

54 Agrar-Umweltprogramme (AES) sind in ganz Europa eingerichtet worden mit dem Ziel, die
55 Auswirkungen von Habitatverlusten in Agrarökosystemen für eine Reihe von
56 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 Geschlechtstiere 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 der 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 Sammelfernung 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 umgebende 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

85

86 **Introduction**

87 Population declines in many native species within agro-ecosystems have been
88 attributed partly to the loss and fragmentation of suitable habitats resulting from agricultural
89 intensification (Tilman, Fargione, Wolff, D'Antonio, Dobson et al. 2001; Winfree, Aguilar,
90 Vazquez, LeBuhn & Aizen 2009). To mitigate these declines, a number of government-
91 funded agri-environment schemes (AES) have been implemented (European Economic
92 Community regulation 2078/92). These compensate farmers for undertaking farming
93 practices considered favourable to biodiversity, including less intensive management within
94 cropped areas and creating new habitats on uncropped land. AES have been shown to
95 benefit birds, bees, butterflies, and plants, leading to increased species richness and
96 abundance of individuals on focal habitat patches (Carvell, Meek, Pywell, Goulson &
97 Nowakowski 2007; Pywell, Heard, Bradbury, Hinsley, Nowakowski et al. 2012; Pywell, Meek,
98 Loxton, Nowakowski, Carvell et al. 2011). However, there has been much debate as to
99 whether these local-scale benefits translate to effects on long-term declines in farmland
100 biodiversity (Carvalho, Kunin, Keil, Aguirre-Gutiérrez, Ellis et al. 2013; Kleijn & Sutherland
101 2003). In particular, there is little evidence for positive effects of AES on reproduction and
102 population persistence of key taxa.

103 Bumblebees are a group of conservation concern globally, having undergone
104 widespread declines in range and diversity over recent decades (Cameron, Lozier, Strange,
105 Koch, Cordes et al. 2011; Williams & Osborne 2009). They are key pollinators of native plant
106 species and a variety of crops and, together with other wild bees, may provide insurance
107 against honey bee declines (Garibaldi, Steffan-Dewenter, Winfree, Aizen, Bommarco et al.
108 2013; Garratt, Coston, Truslove, Lappage, Polce et al. 2014; Winfree, Williams, Dushoff &
109 Kremen 2007). Bumblebees are eusocial insects with (in temperate regions) an annual
110 colony cycle. Queens establish colonies in spring and their ability to produce new sexuals
111 (males and queens) at the end of the cycle is largely dependent on the availability of floral
112 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 & Tschardtke 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 \pm 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*

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

401

402 **Discussion**

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

418

419 Our results may have been influenced by one species in particular, *Bombus lapidarius*,
420 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.

556

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565

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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723 **Figure captions**

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

730

731 **Fig. 2.** Index of bumblebee sexual biomass (MQ, see text), at the landscape scale on
732 conventionally managed margins of fields surrounding sown flower patches of different sizes
733 (0.25 ha, 0.5 ha, 1 ha) and unsown controls. Results shown are means (per 100 m transect,
734 per survey) of predicted values from minimal adequate models in Table 1B with standard
735 errors calculated from data aggregated at the level used in statistical analyses. 'Size diff' =
736 significance of differences between the three sown patches of different size; *** $P<0.001$;
737 ** $P<0.01$; NS = not significant.

738

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

745 **Fig. 4.** Relationships between predicted bumblebee sexual biomass (MQ) per 100 m at each
746 site on landscape transects surrounding sown flower patches of different sizes and the
747 proportion of arable land, for (A) total *Bombus*, (B) *Bombus lapidarius*, (C) *Bombus*
748 *pascuorum* and (D) *Bombus terrestris* agg.. Curves representing different patch sizes were
749 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. ¹Effects of patch type relate to differences between sown and
 754 control patches, with identical effects at all sown patches. ²Effects 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 ³Floral 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	Total <i>Bombus</i>			<i>B. lapidarius</i>		<i>B. pascuorum</i>		<i>B. terrestris</i> agg.	
	df	F	P	F	P	F	P	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	Total <i>Bombus</i>			<i>B. lapidarius</i>		<i>B. pascuorum</i>		<i>B. terrestris</i> agg.	
	df	F	P	F	P	F	P	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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761 **Table 2.** Regression statistics for linear models relating total biomass of bumblebee sexuals
 762 (MQ) to the proportion of arable land within 1000 m of each patch.

Transect type			Total <i>Bombus</i>	<i>B. lapidarius</i>	<i>B. pascuorum</i>	<i>B. terrestris</i> 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
		<i>P</i>	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
		<i>P</i>	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
		<i>P</i>	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
		<i>P</i>	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
		<i>P</i>	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
		<i>P</i>	0.206	0.110	0.287	0.483

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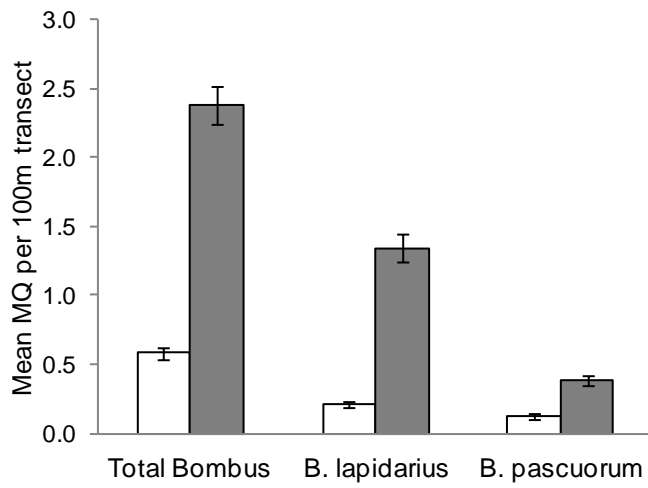
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766 **Fig. 1**

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Fig. 2.

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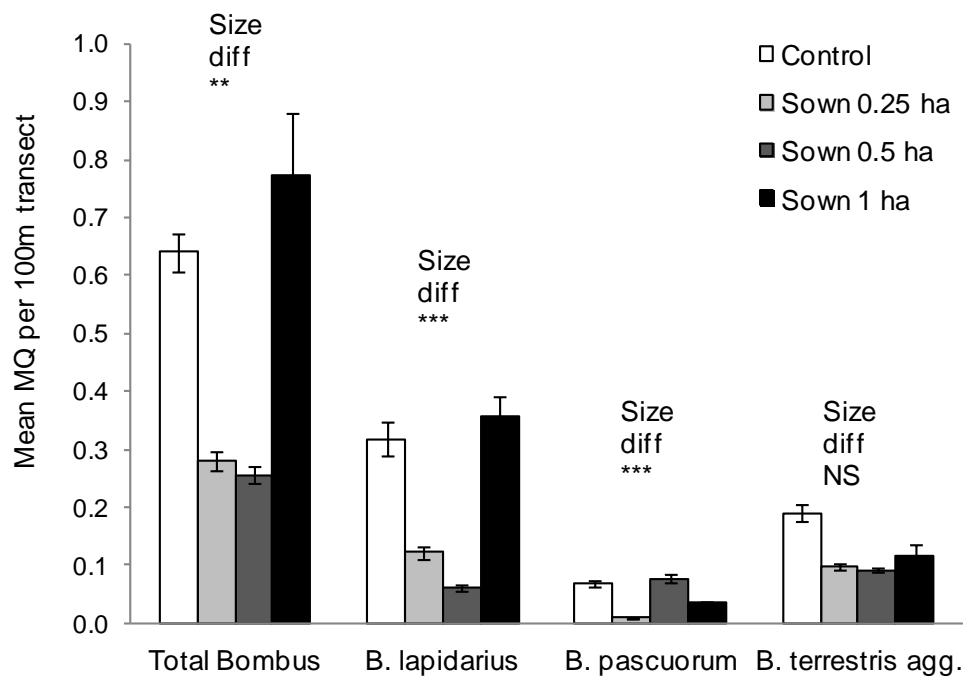
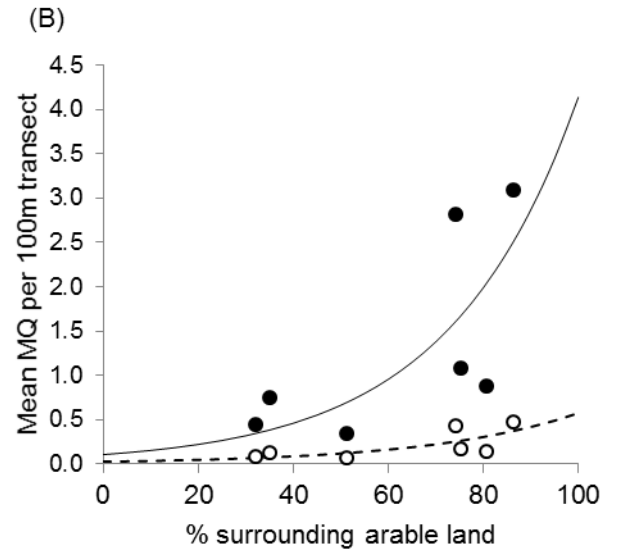
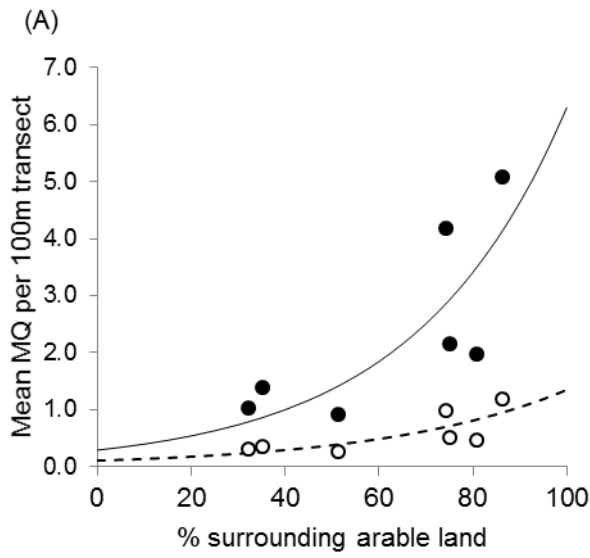
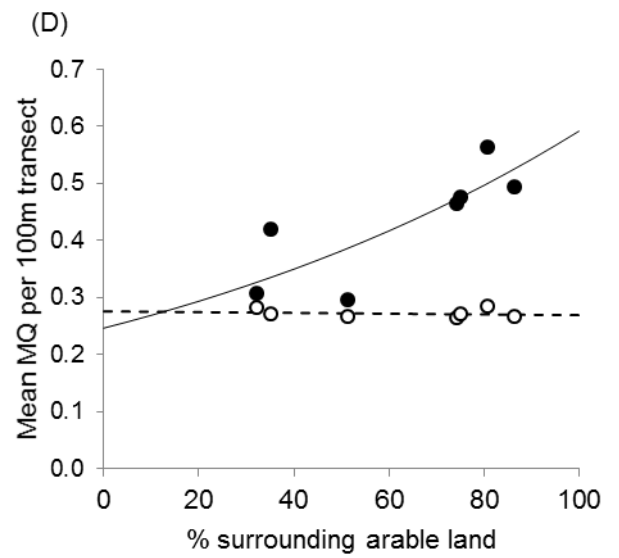
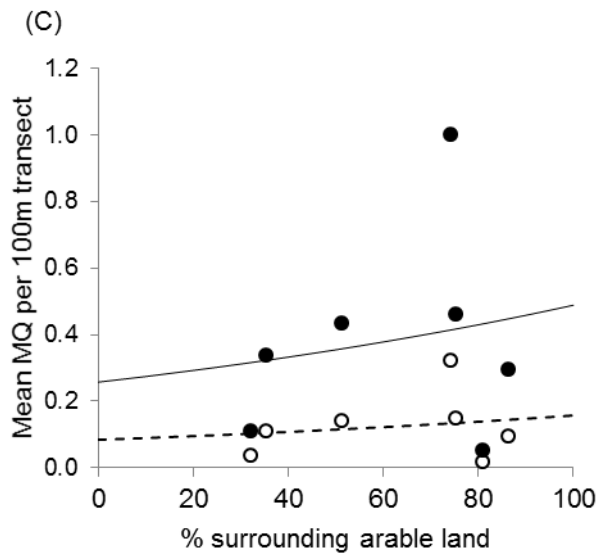


Fig. 3.



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Fig. 4

