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Modest enhancements to conventional grassland diversity improve the provision of pollination services

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Summary

1. Grassland for livestock production is a major form of land use throughout Europe and its intensive management threatens biodiversity and ecosystem functioning in agricultural landscapes. Modest increases to conventional grassland biodiversity could have considerable positive impacts on the provision of ecosystem services, such as pollination, to surrounding habitats.

2. Using a field-scale experiment in which grassland seed mixes and sward management were manipulated, complemented by surveys on working farms and phytometer experiments, the impact of conventional grassland diversity and management on the functional diversity and ecosystem service provision of pollinator communities were investigated.

3. Increasing plant richness, by the addition of both legumes and forbs, was associated with significant enhancements in the functional diversity of grassland pollinator communities. This was associated with increased temporal stability of flower–visitor interactions at the community-level. Visitation networks revealed pasture species *Taraxacum sp. (Wigg.)* and *Cirsium arvense (Scop.)* to have the highest pollinator visitation frequency and richness.

4. Increased sward richness was associated with an increase in the pollination of two phytometer species; *Fragaria × ananassa* and *Silene dioica*, but not *Vicia faba*. Enhanced

59 functional diversity, richness and abundance of the pollinator communities associated with
60 more diverse neighbouring pastures were found to be potential mechanisms for improved
61 pollination.

62

63 *5. Synthesis and applications.* A modest increase in conventional grassland plant diversity
64 with legumes and forbs, achievable with the expertise and resources available to most
65 grassland farmers, could enhance pollinator functional diversity, richness and abundance.
66 Moreover, our results suggest that this could improve pollination services and consequently
67 surrounding crop yields (e.g. strawberry) in agro-ecosystems.

68

69 **Key-words:** agro-ecosystems, crop yields, ecosystem services, functional diversity, grassland
70 diversity, plant richness, pollinators, visitation networks.

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87 **Introduction**

88 Understanding how species' interactions affect ecological function is central to conservation
89 biology. For sustainable land management, land managers can engineer community

90 composition through inter-trophic relationships to enhance ecosystem services. Examples
91 include providing food for pollinators (Potts *et al.* 2003) to enhance crop pollination and
92 providing alternative prey for predatory insects (Symondson, Sunderland & Greenstone
93 2002) which provide pest control. Manipulating basal trophic levels has been shown to have
94 significant bottom-up effects on higher trophic-level diversity and ecosystem functioning
95 (Novotny *et al.* 2006; Haddad *et al.* 2009; Scherber *et al.* 2010). A diverse plant community
96 provides opportunities for niche diversification and coexistence of associated species
97 (Novotny *et al.* 2006; Rzanny & Voigt 2012), with a diversity of functional traits (Hooper *et al.*
98 *al.* 2005) which has been found to improve ecosystem service provision (Albrecht *et al.*
99 2012). This positive relationship between functional diversity and ecosystem service
100 provision is associated with complementary niche partitioning between functional groups
101 which can enhance the temporal and spatial stability of ecosystem processes (Naeem & Li
102 1997; Ebeling *et al.* 2008; Macfadyen *et al.* 2011; Brittain, Kremen & Klein 2013). This is true
103 for the stability of pollination services; if complementary pollinator functional groups visit
104 different plant species, or the same plant species at different times, this can enhance the
105 overall visitation and pollination of plant communities (Hoehn *et al.* 2008; Albrecht *et al.*
106 2012; Brittain, Kremen & Klein 2013). Functional facilitation can also occur, for example
107 interactions between pollinators may force individuals to move from plant to plant
108 facilitating cross-pollination (Greenleaf & Kremen 2006). Furthermore, communities with
109 high functional diversity are more likely to include functionally effective individuals or
110 groups (Albrecht *et al.* 2012). Although a number of hypotheses explain such cascading
111 ecosystem-level processes (Hooper *et al.* 2005), much of the work has been theoretical and
112 the putative causal factors rarely manipulated in the field at the community-scale.

113
114 In this study conventional grasslands used for livestock production provide a model system
115 to determine how manipulation of basal trophic levels (by modest increases in sward
116 richness and concomitant cutting and grazing treatments) affects pollination. Few studies
117 have focussed on ecosystem service provision by conventional grasslands (Potts *et al.* 2009;
118 Power & Stout 2011). Moreover, grassland agri-environment schemes have had limited
119 effect in diversifying these homogeneous habitats to enhance pollination (Kleijn &
120 Sutherland 2003; Scheper *et al.* 2013). Whilst it is unrealistic to restore managed grasslands
121 to their former high diversity, as they are a product of low-intensity farming systems (van

122 Dijk 1991), modest changes to grassland biodiversity via agri-environment schemes could
123 have extensive benefits due to its widespread cover (grasslands covers 30–40% of European
124 agricultural areas (Sokolović, Radović & Tomić 2011)). Moreover, spillover of pollinators
125 from grasslands to surrounding habitats could enhance pollination at the landscape-scale
126 (Klein, Steffan-Dewenter & Tscharntke 2003; Kremen *et al.* 2004).

127
128 There are three objectives to our study: i) to determine the impact of grassland plant
129 richness and management (cutting and grazing) on pollinator functional diversity and the
130 consequence of functional diversity on the temporal stability of community flower–visitor
131 interactions over the season; ii) to determine which grassland plant species provide
132 disproportionate support to pollinators in terms of the number and richness of visitors, thus
133 providing target species for restoration projects and iii) to determine if increased pasture
134 plant richness is associated with enhanced pollination services as measured by seed/fruit
135 set, weight and quality of three phytometer species. In the context of these objectives,
136 functional diversity is defined as ‘measuring functional trait diversity, where functional traits
137 are components of an organism’s phenotype that influence ecosystem-level processes’
138 (Petchey & Gaston 2006).

139

140 **Materials and methods**

141 Three approaches were used: a field experiment with replicate treatment plots; a
142 correlative approach which used a pre-existing gradient of pasture plant diversity on
143 multiple farms; and a phytometer approach whereby three plant species were placed
144 adjacent to pastures to assay pollination spillover.

145

146 **1) THE FIELD EXPERIMENT**

147 We assessed the impact of manipulating conventional grassland sward diversity and
148 management on pollinator communities using a replicated field-scale experiment from
149 May–September 2011. This was carried out at Rothamsted Research, North Wyke, Devon,
150 UK (50°46′N 3°54′W). A split-plot design was used with four replicate blocks to investigate
151 the effect of two treatments: sward diversity and sward management (Fig. S1 and Fig. S2 in

152 Supporting Information). Two plot sizes were used: 0.1 ha (grazed plots) and 0.07 ha (cut
153 plots).

154

155 Sward diversity was manipulated by sowing three seed mixes; grass only, grass–legume and
156 grass–legume–forb (Table S1 and S2 for species lists). Species were selected from a review
157 of the biodiversity and agronomic value of grassland species by Mortimer *et al.* (2006) as
158 potential target species for agri-environment scheme seed mixes. Each sward diversity
159 treatment was split into two sub-plots which were subjected to one of two management
160 regimes: i) Grazing: grazing by cattle from April/May to early June, no grazing from early
161 June to August, and moderate grazing by cattle from August–October (2 animals per 0.1-ha
162 plot); ii) Cutting: cut early June, grazing by cattle from late August–October.

163

164 **Sampling of pollinators and flowering plants**

165 Plant and pollinator surveys were carried out within a 500-m² sampling area in the centre of
166 each plot by zig-zag walking for 25 minutes catching all insects observed on flowers. Each
167 plant-pollinator ‘visitation interaction’ was recorded (Table S3) by identifying the plant
168 species in the field and collecting the visitor for later identification by taxonomists. Flower-
169 visiting Hymenoptera, Lepidoptera, Coleoptera and Diptera were collected; all four orders
170 carry pollen (Orford, Vaughan & Memmott 2015). All plots within a block (six sub-plots
171 including all treatment combinations (Fig. S1, S2)) were sampled in a random order per day
172 (09.00–17.00h) during warm, dry conditions. Between May–September each of the four
173 blocks were sampled 24 times; each sward type 192 times and management type 288 times
174 (Fig. S1). Following each survey the number of floral units of each plant species was counted
175 along a 25 × 2-m transect in each plot.

176

177 **2) FARM SURVEYS**

178 To increase the spatial scale of our study, and to measure pollinator population-level
179 responses, we investigated the effect of pasture plant species richness across ten
180 independent farms (separated by at least 6.5 km) across south-west England, scattered
181 north and south of Bristol and Bath (map Fig. S3). All were mixed farms, with arable crops
182 and pasture. The farms were selected as they were used in a previous study (Macfadyen *et*
183 *al.* 2009) and therefore data on their management and pasture plant diversity was available.

184 Two pasture fields per farm (20 fields in total) were selected based on their plant species
185 richness to cover a gradient of diversity. Richness was measured using two 30 × 2-m
186 transects where 1–10 species= ‘low’ diversity, 11–20 species= ‘intermediate’ diversity and
187 21–30 species= ‘high’ diversity. Abiotic factors and surrounding landscape features, as well
188 as differing management, are potential causes of each pastures’ plant richness. The pastures
189 had similar management; all were grazed by cattle, used herbicides to spot-spray
190 undesirable species, including *Rumex*, *Cirsium*, and *Senecio* sp., and used nitrogen-based
191 fertilizers. All fields had hedgerows and field sizes are included in Table S4. While detailed
192 information on the surrounding landscape was not recorded, we know it is dominated by
193 agricultural land with some woodland cover. Data on local pesticide use was not available;
194 however, none of the farms were organic so pesticides are likely to have been used. Plant-
195 pollinator surveys were carried out on each pasture five times between May–August 2012,
196 following the same survey protocol as the field experiment (i.e. zig-zag walking within a
197 central 500-m² area for 25 minutes).

198

199 **3) PHYTOMETER EXPERIMENT**

200 Plant phytometers were used to bioassay the pollination service of the pasture on each of
201 the ten farms. During their flowering period, five individuals of each phytometer species,
202 strawberry variety “Symphony”, *Fragaria × ananassa*, (Duch.): Rosaceae; broad bean variety
203 “Sutton”, *Vicia faba* (L.): Fabaceae and red campion *Silene dioica* ((L.) Clairv.):
204 Caryophyllaceae, were positioned at the margin of one pasture field in each farm in early
205 June 2013. As red campion is dioecious five male plants were put out on the farms in
206 addition to the five female plants. Prior to the experiment the strawberry and bean plants
207 were grown from seed in greenhouses until flowering and red campion plants, which were
208 approximately 3-years-old, were stored in polytunnels. Phytometers were relocated to the
209 farms whilst in bud.

210

211 Strawberry is a crop commonly grown in the UK. The plants are self-compatible and while
212 both wind and self-pollination occur, cross-fertilization is favoured (Free 1993). A wide
213 diversity of insects visit strawberry flowers due to their open structure (Dimou *et al.* 2008;
214 Klatt 2013). Strawberries have increased weight and fewer deformities if insect-pollinated
215 (Chagnon, Gingras & Deoliveira 1989; Free 1993; Dimou *et al.* 2008; Klatt 2013). Broad bean

216 is another crop commonly grown in the UK. It has partial cross-fertilization with significantly
217 higher seed numbers and weight when insect-pollinated (Free 1966; Aouar-Sadli, Louadi &
218 Doumandji 2008). Broad bean has closed papilionaceous flowers that only pollinators with
219 long and strong mouthparts can access, predominantly bees (Free 1966; Free 1993; Aouar-
220 Sadli, Louadi & Doumandji 2008). Red campion is a wildflower present in hedgerows and
221 woodlands in the study region. It is dioecious, requires insect pollination and seed-set is
222 related to the amount and identity of pollen deposited on the stigmas (Montgomery, Soper
223 & Delph 2010). It is pollinated by insects with long mouthparts including bees, hoverflies
224 and butterflies (Charlton 2013).

225

226 Location of the phytometer plants was prioritized to ensure that surrounding features were
227 similar between farms e.g. hedgerows and tree cover. Plants were put in areas where
228 disturbance by cattle/tractors was minimal. Wild specimens of the phytometer species were
229 not found in close proximity. Chicken wire fences protected the plants from grazing animals
230 and the phytometers were left in the field for two weeks to allow pollination. Four plant-
231 pollinator surveys were carried out in the centre of the associated pasture field during this
232 period following the same protocol as the plot experiment surveys where a zig-zag walk was
233 carried out within a 500-m² area over 25 minutes.

234

235 In late June the phytometer plants were collected from the farms and kept in enclosed
236 polytunnels to allow fruits to mature. Any new flower buds were removed. Strawberry fruits
237 were picked when ripe and weighed. Mean fruit weight was calculated per farm. Each fruit
238 was classed based on commercial deformity grades (European Commission (2007)) where
239 fruits without or with slight aberrations were sorted into Class 1, whereas severe
240 aberrations lead to Class 2 classification. Broad bean seed pods were collected at maturity
241 and the seeds were counted and weighed; mean seed count (per pod) and seed weight
242 were calculated per farm. Bean plants were still young when harvested. Seed capsules of
243 red campion were collected and the number of seeds per capsule counted and a mean
244 calculated per farm.

245

246 **ANALYSIS**

247 **Objective 1: The impact of plant richness and grassland management on pollinator**
248 **functional diversity and the resulting temporal stability of flower visitation**

249 Pollinator functional diversity of each plot of the field experiment and each field of the farm
250 surveys was calculated. Functional diversity was based on the feeding niche of the pollinator
251 species recorded, which we based on the plant families that each species is known to visit.
252 This was to ascertain the potential complementarity of diets within the pollinator
253 communities. The feeding niche of each pollinator species recorded was determined from
254 the interactions recorded in the current study and by a literature search. This established
255 the pollinator community's potential visitation to plants not just within the grassland but to
256 surrounding habitats. The search was carried out using ISI web of knowledge, the BSBI data
257 base and English Nature reports and included studies from 1883–2010. This added 2398
258 flower–insect interactions to the 143 interactions from the field experiment data and 2189
259 interactions to the 84 interactions observed in the farm surveys.

260

261 Using these interaction data, a functional dendrogram was created in R (R Core
262 Development Team (2012)) for the field experiment and another for the farm surveys by
263 calculating pairwise distances between pollinator species and then using a clustering
264 algorithm (Petchey & Gaston 2007). This was based on similarities in feeding niche of the
265 pollinators (plant families had a binary score; either visited or not visited by the pollinator
266 species) to describe the functional relationships between the pollinator species recorded.
267 Functional diversity was calculated for each plot/field as the total branch length of the
268 functional dendrogram between all the species sampled (Petchey & Gaston 2007) using the
269 'jaccard index' (ade 4 package) (Dray & Dufour 2007) and 'treedive' (vegan package)
270 (Oksanen *et al.* 2012) functions. Values for functional diversity do not have a directly
271 interpreted meaning but provide a means of comparison; the higher the functional diversity
272 the greater the complementarity in feeding niches of the pollinator community and the
273 lower the redundancy. Pollinator species richness (count of species) and abundance (count
274 of individuals) of the plots/fields was calculated to test if differences in functional diversity
275 were distinct from differences in pollinator species richness or abundance.

276

277 The coefficient of variation of visitation (CV) was used as a measure of the temporal
278 variability in the visitation interactions between all plants and pollinators surveyed over the

279 entire sampling season to determine the temporal stability of the potential ecosystem
280 service (adapted from Macfadyen *et al.* (2011)). For the field experiment the data set was
281 separated into six time periods. The CV per plot was calculated across the six time periods as
282 the standard deviation in number of visitation interactions divided by the mean number of
283 visitation interactions. For the farm surveys the CV was calculated for each field with the
284 data set split into five sampling periods.

285

286 To compare pollinator functional diversity, pollinator species richness, pollinator abundance
287 (response variables) between plots of the field experiment, general linear mixed-effects
288 models were used (GLMM; 'lme4' in R (Bates, Maechler & Bolker 2012)). Plot treatments
289 'sward type' and 'management' (and their interaction) were fixed factors. 'Sward type' and
290 'block' were treated as nested random factors to account for the arrangement of the plots.
291 Models were compared with maximum likelihood ratio tests, following model simplification,
292 to evaluate the significance of the predictors on the response variable (Zuur *et al.* 2009).
293 Post-hoc Tukey tests (Hothorn, Bretz & Westfall 2008) were used to determine where
294 differences in the response variable lay between sward types (package 'multcomp' Torsten,
295 Bretz & Westfall 2008). Plots of the residuals were used to check the fits of the models. A
296 GLMM with the same random effects structure was used to test the relationship between
297 CV (response) and pollinator functional diversity (predictor) within the plots. For both the
298 field experiment and farm surveys, correlation coefficients were calculated between
299 pollinator functional diversity, species richness and abundance to assess the degree of co-
300 linearity.

301

302 To determine the relationship between pollinator functional diversity, pollinator species
303 richness, pollinator abundance (response variables) and plant species richness in the farm
304 surveys, GLMMs were also fitted. Plant species richness was treated as a fixed effect and
305 farm was treated as a random factor (to account for abiotic and management differences).
306 Subsequent models were fitted omitting the predictor variable (intercept-only model). The
307 two models were compared with a likelihood ratio test. This method was also used to test
308 the relationship between CV (response) and pollinator functional diversity (predictor) within
309 the fields.

310

311 **Objective 2: Which grassland plant species have disproportionately positive effects upon**
312 **pollinator abundance and diversity?**

313 A quantitative plant-pollinator visitation network of the interactions recorded was created
314 for both the field experiment and farm surveys. Following Hegland *et al.* (2010) we consider
315 the functional value of a species to depend on its interaction frequency and interaction
316 richness (the number of visitors and the number of visitor species respectively); the greater
317 the interaction frequency and richness, the more functionally valuable the plant species.
318 Floral abundance was accounted for by dividing the number of interactions by the number
319 of floral units of each species.

320

321 **Objective 3: The impact of pasture plant species richness on the pollination of crop and**
322 **wildflower species.**

323 Linear regression was used to test for relationships between pasture plant species richness
324 and the phytometer response variables; strawberry fruit weight (mean fruit weight per
325 farm) and deformity (the proportion of Class 1 fruits per farm, arcsine-square-root
326 transformed), mean broad bean seed count (per pod) and weight, per farm. A generalized
327 linear model (GLM) with Poisson errors assessed the relationship between plant species
328 richness and seed count (mean seed count per capsule per farm) of red campion. Pollinator
329 functional diversity was calculated for the 2013 pollinator surveys. Linear regression tested
330 the relationship between plant species richness and pollinator functional diversity.

331

332 Three alternative predictor variables – pollinator functional diversity, abundance and
333 species richness (associated with the neighbouring pasture) – were investigated as potential
334 mechanisms behind any increased pollination of the strawberry phytometers (response
335 variables listed above), using linear regression. A GLM with Poisson errors was used in
336 association with red campion seed count. The differences in AIC values were calculated as a
337 means of comparing the three alternative models for each phytometer response variable
338 (Burnham & Anderson 2004).

339

340 **Results**

341 **Objective 1: The impact of sward diversity and management on pollinator functional**
 342 **diversity and the resulting temporal stability of flower visitation.**

343 In the field experiment 4169 flower visitors were collected comprising 166 insect species: 12
 344 bee species, 34 hoverfly species, 90 non-hoverfly Diptera species, 18 Coleoptera species and
 345 2 Lepidoptera species (Table S5). In the 2012 farm surveys a gradient of 9–36 plant species
 346 per 60 m² was recorded and 1530 flower visitors were collected, comprising 146 insect
 347 species: 15 bee species, 15 hoverfly species, 76 non-hoverfly Diptera species and 23
 348 Coleoptera species (Table S6).

349
 350 Pollinator functional diversity significantly increased as sward diversity increased in the field
 351 experiment ($\chi^2=125.57$, d.f.=1, $P=0.0052$) (Fig 1a). The difference was between grass only
 352 and grass–legume–forb plots ($z=3.61$, d.f.=7 $P<0.001$) (Fig 1a). There was no significant
 353 difference in pollinator functional diversity between cut and grazed management
 354 ($\chi^2=123.22$, d.f.=1, $P=0.13$). No significant difference in pollinator species richness was found
 355 between sward types ($\chi^2=155.97$, d.f.=1, $P=0.069$) or management type ($\chi^2=153.25$, d.f.=1,
 356 $P=0.099$). Sward type did have a significant effect on pollinator abundance ($\chi^2=264.24$,
 357 d.f.=1, $P=0.026$) being higher in grass–legume–forb plots than grass only plots ($z=2.98$,
 358 d.f.=7, $P=0.0081$). Management type did not have any significant effect on pollinator
 359 abundance ($\chi^2=261.01$, d.f.=1, $P=0.072$).

360
 361 In the farm surveys pollinator functional diversity was significantly positively associated with
 362 plant species richness ($\chi^2=14.542$, d.f.=1, $P<0.001$) (Fig. 1b) as was pollinator species
 363 richness ($\chi^2=10.831$, d.f.=1, $P<0.001$) and pollinator abundance ($\chi^2=9.178$, d.f.=1, $P=0.002$).

364
 365 In both the field experiment and farm surveys the response variables; pollinator functional
 366 diversity, species richness and abundance, were collinear ($r \geq 0.77$; Table S7). However, they
 367 responded differently to some of the treatments (e.g. pollinator functional diversity c.f.
 368 pollinator species richness) and so are considered separately.

369
 370 It could be argued that high pasture plant species richness indicates management that is
 371 generally 'sympathetic' to biodiversity across the farm and so pollinator communities could
 372 have been responding to farm-scale rather than field-scale management. We used a

373 Wilcoxon matched-pairs signed-ranks test where fields were paired per farm to test if the
374 fields differed in pollinator functional diversity, thereby removing the farm effect. There was
375 a significant difference between fields of the same farm ($V=50$, $n=10$, $P=0.02$), hence
376 variation in pollinator communities was not due to farm-scale management but to individual
377 fields.

378
379 A significant linear negative relationship existed between the functional diversity of the
380 pollinator community and the temporal variability of insect–flower visitation in both the
381 field experiment ($\chi^2=21.70$, d.f.=1, $P<0.001$) (Fig. 1c) and farm surveys ($\chi^2=11.86$, d.f.=1,
382 $P<0.001$) (Fig. 1d). Thus, as pollinator functional diversity increases, the temporal stability of
383 flower visitation increases.

384

385 **Objective 2: Which grassland plant species have disproportionately positive effects on**
386 **pollinator abundance and diversity?**

387 In the field experiment *Taraxacum sp.* (F. H. Wigg.) was the most important species for
388 supporting pollinators (per floral unit), attracting 35% of all pollinator visits and 33% of all
389 pollinator species, followed by *Ranunculus acris* (L.) and *Cardamine pratensis* (L.).

390 Surprisingly, grass species including *Alopecurus pratensis* (L.) and *Dactylis glomerata* (L.)
391 were commonly visited by pollinators (Fig. S4a, Table S3), predominantly by Diptera within
392 the Syrphidae and Muscoidea families. To confirm that the insects were feeding on the
393 pollen and verify the grasses as a protein source, a stratified random sample of 60
394 individuals of 23 of the Diptera species caught on the grasses in the field experiment were
395 dissected. In 72% of cases, Poaceae pollen was present in the abdomen, suggesting the
396 dietary importance of grasses to Diptera.

397

398 In the farm surveys *Cirsium arvense* ((L.) Scop.) was found to be the most important species,
399 attracting 17% of all pollinator visits and 18% of all pollinator species followed by *Cirsium*
400 *palustre* ((L.) Scop.) and *Crepis capillaris* ((L.) Wallr.) (Fig. S4b). *Taraxacum sp.* floral units
401 accounted for 0.02% of all floral units within the plots and *Cirsium arvense* floral units
402 accounted for 0.08% of floral units in the farm surveys. Therefore the results are not
403 necessarily a consequence of these species' abundance.

404

405 **Objective 3: The impact of pasture plant species richness on the pollination of crop and**
406 **wildflower species.**

407 In the 2013 pasture surveys (associated with the phytometer experiment), 349 insects were
408 collected comprising 72 insect species: 9 bee species, 17 hoverfly species, 36 non-syrphid
409 Diptera species, 5 Coleoptera species and 3 Lepidoptera species. A gradient of 9–28 plant
410 species per field was recorded per transect (30 × 2-m). With regards to seed/fruit
411 production of the phytometer plants, 161 strawberries were harvested, 136 broad bean
412 seeds were collected from 44 pods and 39 280 red campion seeds were collected from 274
413 seed capsules.

414
415 Pasture plant species richness was significantly and positively associated with strawberry
416 fruit weight ($t=2.86$, d.f.=9, $P=0.021$, Fig. 2) and proportion of Class 1 fruits ($t=4.62$, d.f.=9,
417 $P=0.002$, Fig. 3). Plant species richness was also significantly positively associated with seed
418 count per capsule of red campion ($z=2.79$, d.f.=9, $P=0.005$, Fig. 4). For broad bean there was
419 no significant relationship detected between pasture plant species richness and seed count
420 per pod ($t=-1.28$, d.f.=8, $P=0.24$) or seed weight ($t=-1.43$, d.f.=1,7, $P=0.20$). There was a
421 significant positive relationship between pasture plant species richness and pollinator
422 functional diversity ($t=4.031$, d.f.=1,8, $P=0.004$) as in Objective 1. Pollinator functional
423 diversity, richness and abundance were all responsible for enhanced pollination of the
424 phytometer plants to varying extents (Table 1, Fig. 2, Fig. 3).

425
426 **Discussion**

427 We found modest increases in conventional grassland plant species richness to be
428 associated with significantly enhanced pollination services, potentially enhancing crop yields
429 and wildflower reproduction in adjacent habitats. In what follows we discuss our findings in
430 relation to our original objectives and end by considering practical management options for
431 grassland management in light of our results.

432
433 **Can higher sward diversity enhance ecosystem functioning and services?**

434 In the field experiment both legumes and forbs were needed to create a suitable ecological
435 infrastructure to enhance pollinator functional diversity. Sward richness in the farm surveys

436 was also positively associated with pollinator functional diversity. Complementarity in
437 resource use of the more functionally diverse pollinator communities is a potential
438 mechanism behind the lower temporal variability in flower visitation found at both scales.
439 This has potential implications for a more temporally stable ecosystem service. The fact that
440 relationships found in the field experiment held true in the farm-scale studies, where
441 population responses were measured, supports the use of small-scale experiments with
442 pollinators.

443
444 Increased pollinator functional diversity, species richness and abundance were associated
445 with increased pollination of strawberry. As these pollinator community variables were
446 correlated it is difficult to determine the causative factor behind enhanced pollination.
447 However, AIC values suggested pollinator functional diversity and richness to be equally
448 effective in increasing strawberry weight, whilst richness appeared to have the biggest
449 positive effect on strawberry quality (class) followed by abundance and functional diversity.
450 Spatial complementarity of pollen deposition has been highlighted as a mechanism behind
451 increased strawberry pollination and resulting quality; large and average-sized bees
452 pollinate the apical stigmata and small-sized bees pollinate the basal stigmata (Chagnon,
453 Gingras & Deoliveira 1993). Maximizing fruit weight and quality will achieve the highest
454 prices for growers providing an incentive to encourage these natural ecosystem processes.
455 However, given we use phytometers the results are not directly related to estimates of
456 farm-scale crop production.

457
458 The seed-set of red campion was positively associated with sward richness; this however
459 could not be explained by pollinator functional or species diversity or abundance. The
460 tubular flower structure of red campion is likely to lead to a more specialized pollination
461 syndrome than strawberry. Therefore the diversification of pollinator feeding niches may be
462 redundant. Although many studies focus on the value of natural systems in providing
463 benefits to managed systems, few have considered the value of managed systems in
464 maintaining wildflower pollination (Blitzer *et al.* 2012).

465

466 Pasture plant species richness was not associated with improved pollination of broad bean.
467 The flower of broad bean is even more specialized than red campion and is predominantly
468 pollinated by large bees (Free 1966; Aouar-Sadli, Louadi & Doumandji 2008) and so the issue
469 of redundancy is raised again. It is likely that large bees forage at a scale greater than that of
470 individual pastures and consequently the local effect of increased botanical richness may
471 not translate into enhanced pollination.

472

473 An unexpected outcome of the field experiment was that the pollinator community
474 parameters did not significantly differ between the cut and grazed treatments. One possible
475 reason could be that surrounding landscape features provided a refuge for the pollinators
476 during cutting. The realized plant species composition of the plots (Table S2) show there is
477 not a great difference in the species richness between the cut and grazed plots.

478

479 It is important to note that a limitation of our work was that we utilized a pre-existing
480 gradient of pasture species richness in the farm surveys and therefore a correlative
481 approach; manipulative experiments at the farm-scale are needed to prove the relationship
482 between plant richness and pollination.

483

484 **Which species should be introduced into seed mixes?**

485 *Taraxacum* sp. and *C. arvense* were the most valuable floral resources to pollinators in the
486 visitation networks of the field experiment and farm data respectively. It could be that these
487 species have a high visual appearance to pollinators due to their large flowers.

488 Unfortunately, these species have little agronomic value and may even be detrimental
489 (Mortimer *et al.* 2006). This trade-off between agronomic and biodiversity benefits must be
490 considered in agri-environment schemes and species that provide benefits to the farmer as
491 well as the environment must be identified. We highlight Chicory *C. intybus* a species sown
492 into the experimental plots, as a possible target species. It had high visitation providing
493 resources for pollinators and also agronomic value; it has anti-helminthic properties which
494 result in increased weight gain in lambs (Marley *et al.* 2006) and a deep tap root that
495 captures fertilizers (Moore, Sanford & Wiley 2006).

496

497 **Conclusion**

498 Without widespread changes in the management of improved grasslands, the decline of
499 many pollinator species is likely to continue (Tscharrntke *et al.* 2005; Carvell *et al.* 2006).
500 Manning *et al.* (2015) show that increasing the diversity of grassland plants is likely to be
501 associated with increases in the diversity of a wide range of taxa, with possible conservation
502 and ecosystem service benefits. Our work adds a new aspect to this evidence by
503 demonstrating positive effects on pollination services. Techniques to improve pasture plant
504 species richness are achievable with the expertise and resources available to most grassland
505 farmers. These can include sowing desirable seed mixes, spreading green hay cut from
506 species-rich sites, sward disturbance (e.g. turf removal, harrowing or use of herbicides),
507 sowing hemiparasitic species e.g. *Rhinanthus minor* and reducing phosphorous and
508 potassium levels (Pywell *et al.* 2012). A desirable balance between agronomic performance
509 of the grassland and its diversity must be considered when choosing such management
510 options. The cascading bottom–up effects of plants, seen at two spatial scales here,
511 demonstrates that modest increases in grassland floral richness is an option for land
512 managers wanting to improve the value of their land for pollinators and ultimately enhance
513 pollination in agricultural habitats.

514

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518 Biodiversity Project’. Thanks to taxonomists (National Museum of Wales) and the farmers.
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520

521 **Data accessibility**

522 All data (pollinator surveys, plant surveys and phytometer experiment) are available from
523 the Dryad Digital Repository: doi:10.5061/dryad.tp0d0 (Orford *et al.* 2016).

524

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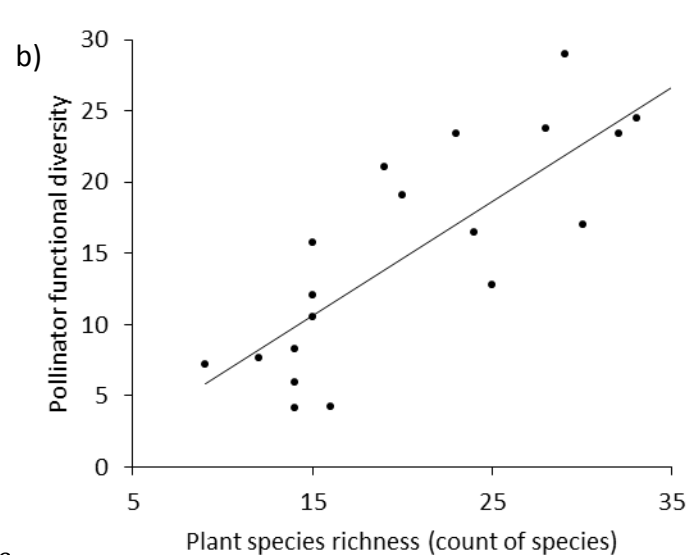
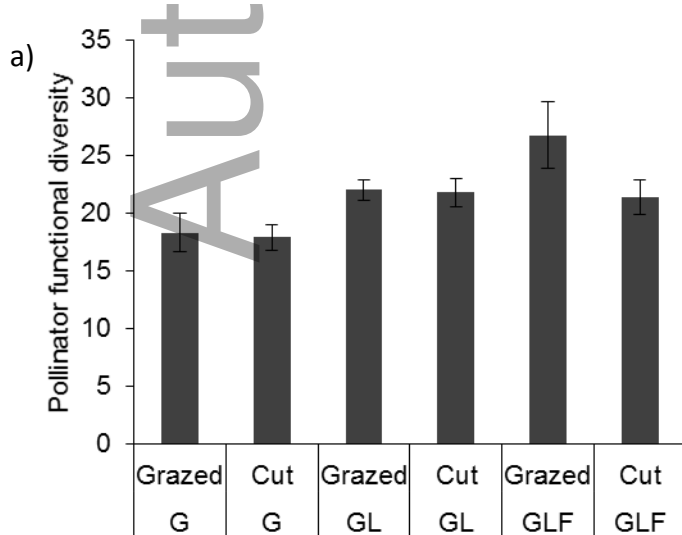
Phytometer measurement (response)	Pollinator community parameter (predictor)	t/z	P	Δ AIC
	Functional diversity	t = 3.25	0.012*	0
Strawberry weight	Species richness	t = 2.84	0.022*	1.44
	Abundance	t = 1.66	0.14	5.47

	Functional diversity	t = 3.2	0.013*	0
Strawberry class	Species richness	t = 4.14	0.0032*	3.25
	Abundance	t = 3.43	0.009*	0.81
	Functional diversity	z = 0.47	0.64	66.29
Red campion seed count	Species richness	z = 1.3	0.19	0
	Abundance	z = 1.04	0.3	65.43

680 Tables and Figures

681 **Table 1.** The results of the linear models (response variables: strawberry weight and class)
 682 and glms (response variable: red campion seed count). 't' is reported for the linear models
 683 and 'z' for the glms. *denotes a significant result

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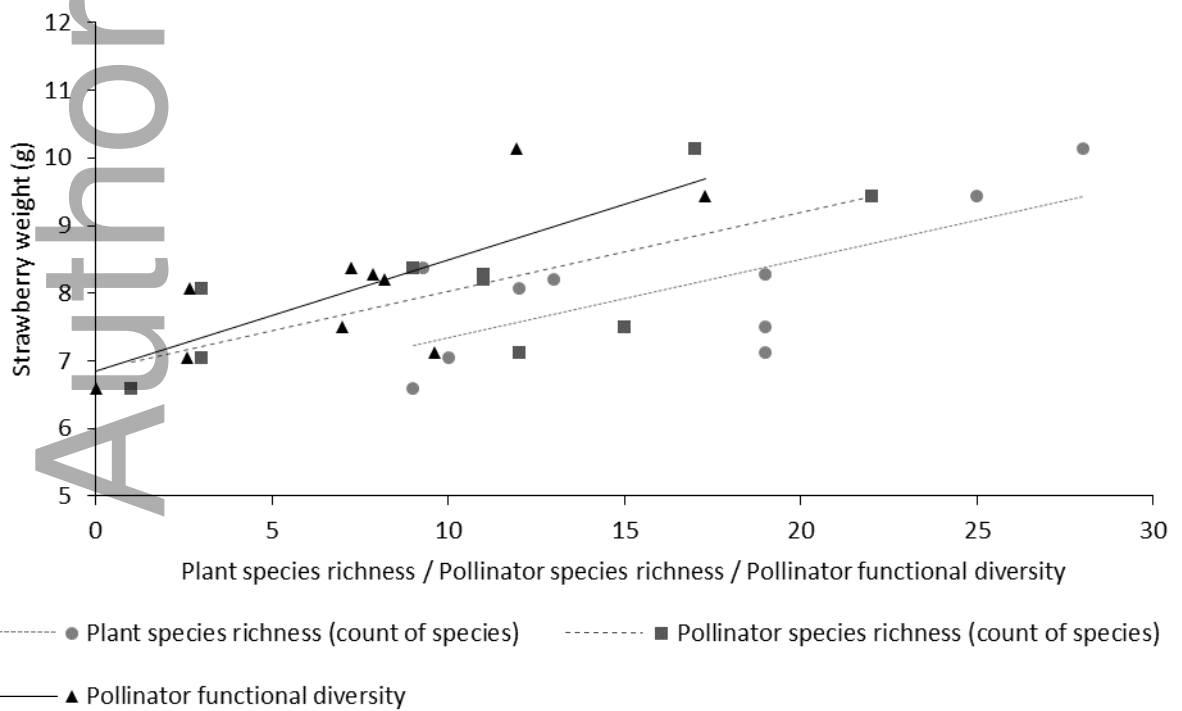


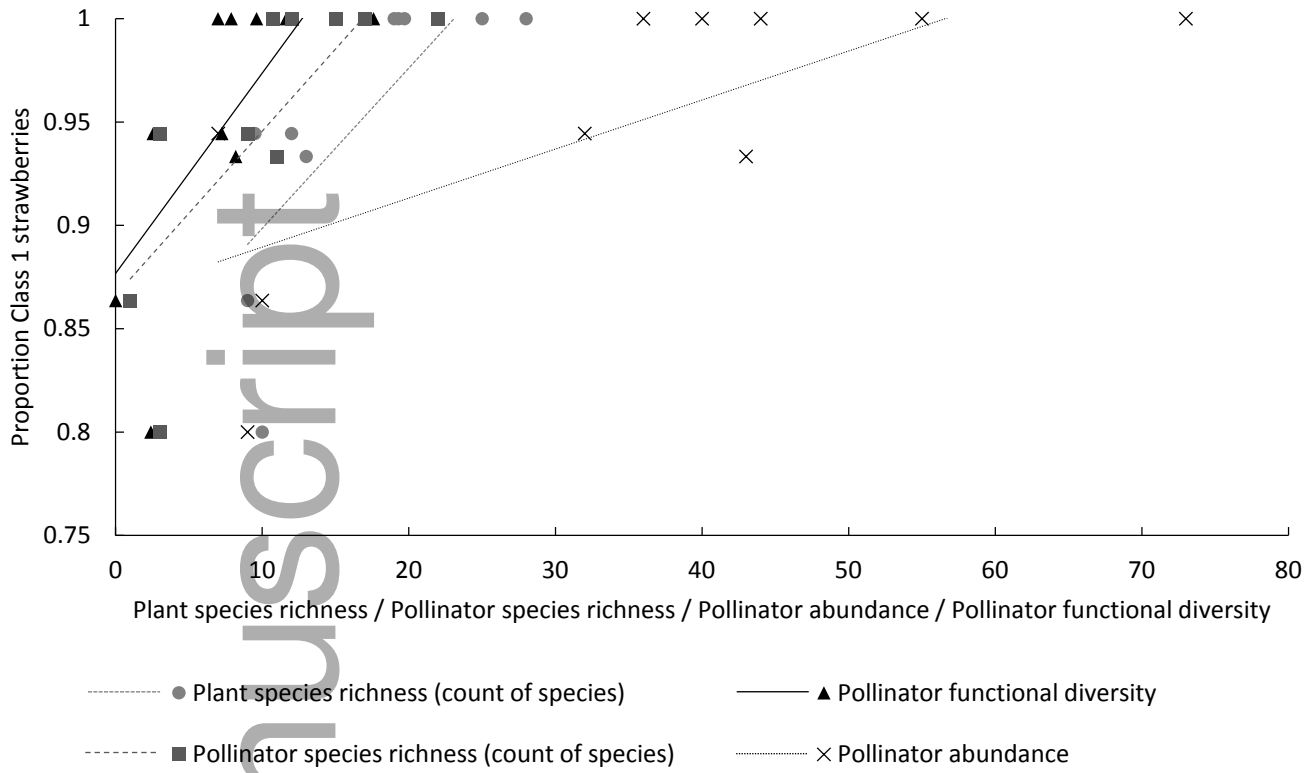
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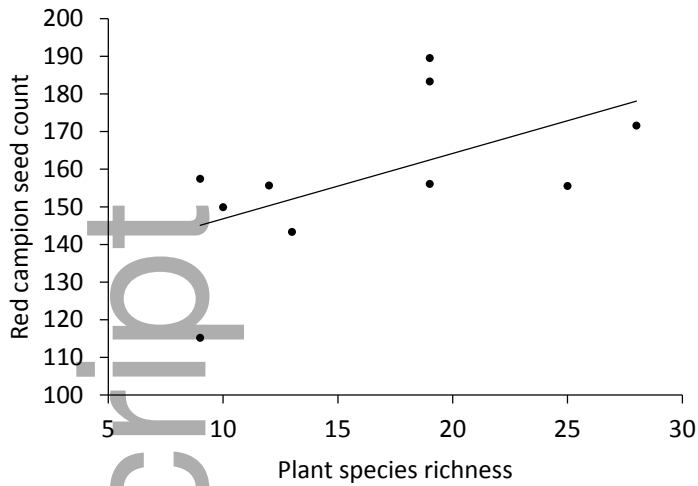
Figure 1.





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Figure 3.



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753 Figure 4.
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771 **Legends**

772 **Figure 1.** a) Pollinator functional diversity in the field experiment: G=Grass; GL=Grass-
773 legume; GLF=Grass–legume–forb; error bars represent standard error. b) Pollinator
774 functional diversity and plant species richness (per 30 x 2-m transects) within the fields of
775 the farm surveys. c) The relationship between pollinator functional diversity and the

776 temporal stability in flower visitation (the coefficient of variation in visitation (CV)) for the
777 field experiment and d) farm surveys.

778

779 **Figure 2.** The relationship of plant species richness, pollinator species richness and pollinator
780 functional diversity of the 10 neighbouring pastures with the mean fruit weight of the
781 strawberry phytometers.

782

783 **Figure 3.** The linear relationship of plant species richness, pollinator species richness,
784 pollinator abundance and pollinator functional diversity of the 10 neighbouring pastures
785 with the proportion of Class 1 strawberry fruits of the phytometers.

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787 **Figure 4.** The relationship between pasture plant species richness and mean seed count of
788 red campion phytometer specimens across 10 farms.

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795 **Supporting Information**

796 Additional Supporting Information may be found in the online version of this article:

797 **Figure S1.** Experimental design of one of the four replicate blocks of the field experiment.

798 **Figure S2.** Layout of the field experiment.

799 **Figure S3.** Locations of the 10 farms.

800 **Figure S4.** Grassland plant species' interaction frequency and interaction richness.

801 **Table S1.** Plant species of the seed mixes of the field experiment.

802 **Table S2.** Realized composition of the three sward types under grazing or cutting
803 management of the field experiment.

804 **Table S3.** Plant species and their insect visitor species.

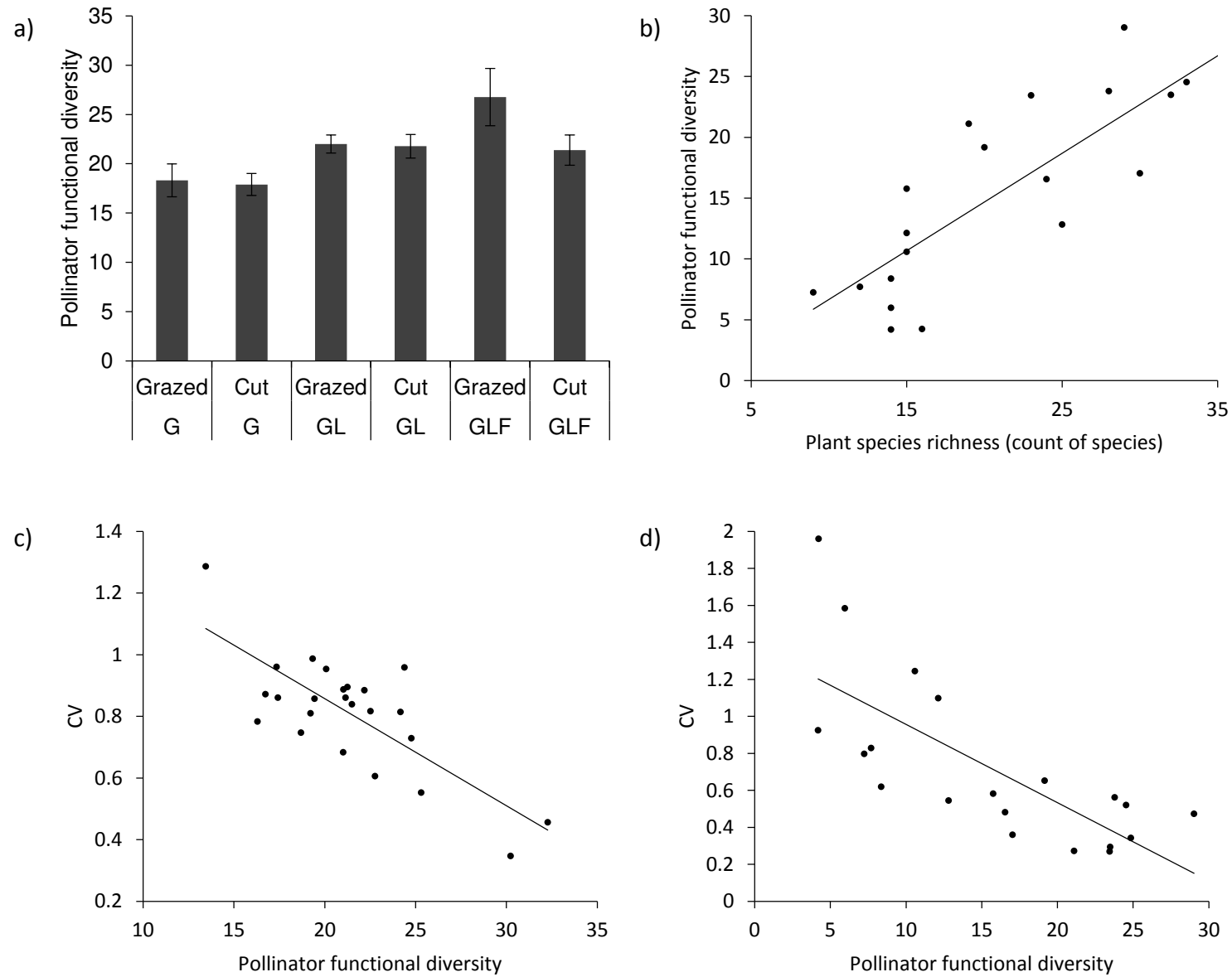
805 **Table S4.** Field sizes.

806 **Table S5.** Pollinator species lists from the different sward types of the field experiment.

807 **Table S6.** Species lists of pollinators found on each farm (2012 and 2013 surveys).

808 **Table S7.** Correlations between the parameters of the pollinator communities in both the
809 field experiment and farm pollinator surveys.

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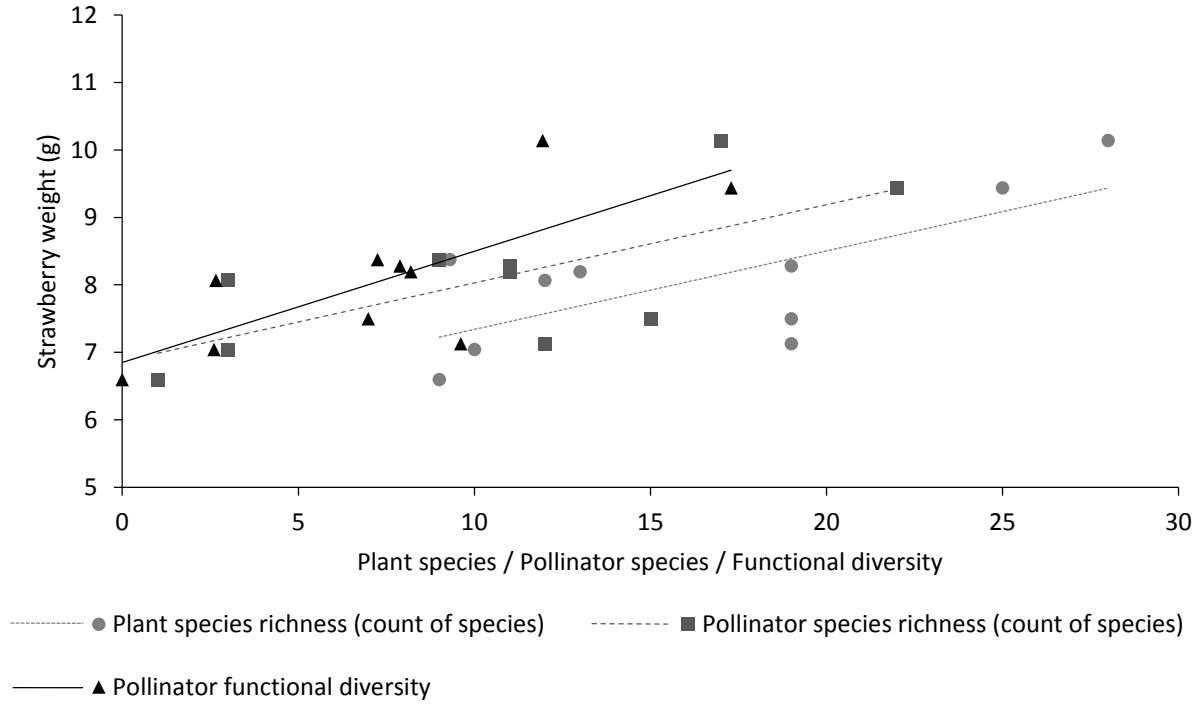


Figure 2.

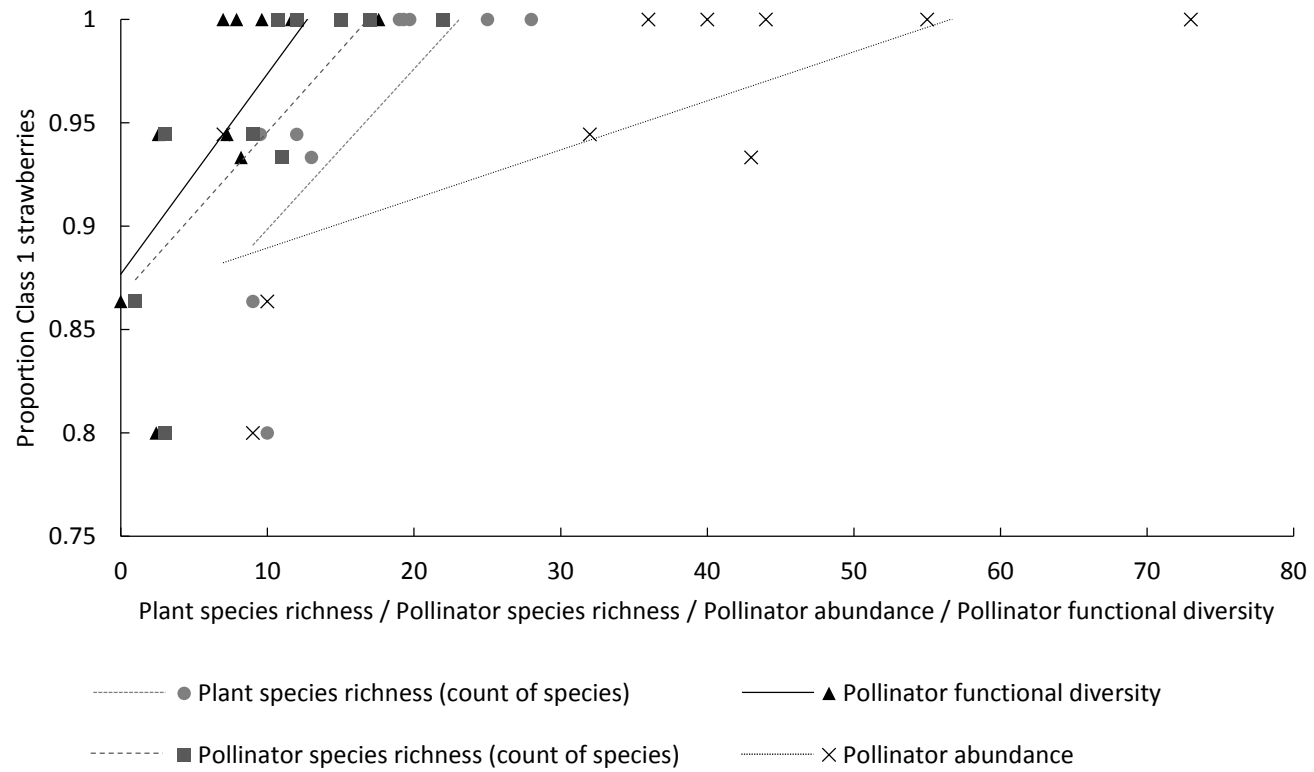


Figure 3.

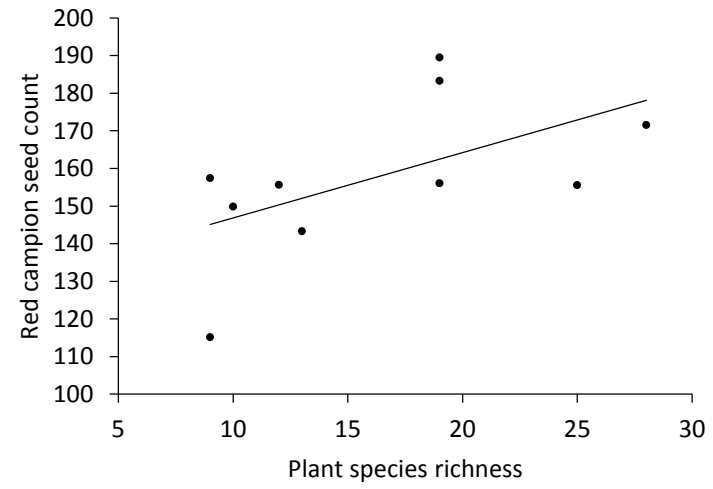


Figure 4.