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25 **Summary**

26

27 Bees, hoverflies and butterflies are taxa frequently studied as pollinators in agricultural and
28 conservation contexts. Although there are many records of non-syrphid Diptera visiting
29 flowers, they are generally not regarded as important pollinators. We use data from 30 pollen-
30 transport networks and 71 pollinator-visitation networks to compare the importance of
31 various flower-visiting taxa as pollen-vectors. We specifically compare non-syrphid Diptera
32 and Syrphidae to determine if neglect of the former in the literature is justified. We found no
33 significant difference in pollen-loads between the syrphid and non-syrphid Diptera.
34 Moreover, there was no difference in the level of specialisation between the two groups in the
35 pollen-transport networks, though the Syrphidae had significantly greater visitation evenness.
36 Flower visitation data from 33 farms showed that non-syrphid Diptera made up the majority
37 of the flower-visiting Diptera in the agricultural studies (on average 82% abundance and 73%
38 species richness), and we estimate that non-syrphid Diptera carry 84% of total pollen carried
39 by farmland Diptera. As important pollinators, such as bees, have suffered serious declines, it
40 would be prudent to improve our understanding of the role of non-syrphid Diptera as
41 pollinators.

42

43 Key words: non-syrphid Diptera, pollinators, pollen-loads, pollen-transport networks,
44 Syrphidae

45

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48

49 **Introduction**

50

51 Pollinators play a crucial role in ecosystems by facilitating plant reproduction [1]. They
52 provide an essential ecosystem service being responsible for 35% of global crop-based food
53 production [2]. Given the recent substantial losses of pollinators [3, 4] induced by habitat
54 loss, altered land use, alien species and climate change [5, 6] there is a real need for land
55 managers to conserve wild pollinator communities.

56

57 Non-syrphid Diptera are diverse, common and ubiquitous in both natural and managed
58 habitats [7, 8], and therefore have the potential to contribute significantly to pollination.
59 Although they are unlikely to be the most important pollinators, *en masse* they could have a
60 larger role than previously realised. Seventy-one families of Diptera contain flower-visitors,
61 and Diptera are regular visitors to at least 555 plant species [9], which include over 100
62 cultivated plant species comprising important crops, such as mango [10], oil seed rape [11],
63 onion [12] and cocoa [13]. Although records of Diptera as flower-visitors exist, evidence of
64 their importance as pollinators is limited.

65

66 Unfortunately, studies of pollinator communities usually focus on bumblebees, honeybees,
67 solitary bees (Hymenoptera), hoverflies (syrphid Diptera) and butterflies (Lepidoptera).
68 Consequently agri-environment schemes and other management strategies are primarily
69 designed to conserve these taxa [14]. Non-syrphid Diptera have received much less attention
70 and are often excluded from key pollination studies [e.g. 4, 6, 15, 16-22] probably because
71 they are difficult to identify and assumed to be unimportant. This assumption is untested
72 however as there have been no community-wide studies quantifying their contribution to
73 pollination. Some visitation network studies do include non-syrphid Diptera [e.g. 8, 23-25]

74 but not all [26], and these rarely measure pollination. Although the neglect of non-syrphid
75 Diptera has been acknowledged [27] there is a paucity of studies which aim to evaluate their
76 relative importance.

77

78 One area where the importance of non-syrphid dipteran pollinators is acknowledged is at high
79 altitudes and latitudes, for example in alpine and subarctic ecosystems where bees are less
80 abundant [8, 28-30]. Additionally the sapromyophilous pollination syndrome
81 (sapromyophiles are attracted to flowers mimicking the odours of dead animals or dung)
82 provides good evidence for a significant role of the non-syrphid Diptera in pollination. This
83 pollination syndrome has shaped the flower morphology of a diverse group of angiosperms
84 [9].

85

86 In this study the potential importance of various flower-visitor taxa as pollinators is compared
87 with data originating from a range of temperate ecosystems including meadows, sand dunes,
88 farmland, heathland and patches of semi-natural vegetation. We estimate their likely
89 importance in farmland habitats in more depth where the ecosystem service of pollination is
90 required for food production. We specifically compare the Syrphid and non-syrphid Diptera
91 to determine if neglect of the latter is justified.

92

93 Visitor identity, visitation, morphology, behaviour, pollen-load, delivery of pollen to stigmas
94 and seed-set are all ways of assessing pollinator importance [9, 31-33]. In this study, we
95 concentrate on the quantitative side of the pollination process sensu Herrera [31] focusing on
96 visitation and pollen-load components. To do this we use data from existing independent
97 visitation and pollen-transport networks. While pollen-transport and visitation do not prove
98 pollination, they are essential prerequisites [34, 35].

100 There are four objectives to our study: 1) To compare pollen-loads (count of grains) of
101 various flower-visiting insect taxa. Following findings by Rader et al. [36] we predicted the
102 Hymenoptera will have the largest pollen-loads relative to other taxa; 2) To compare the non-
103 syrphid Diptera and syrphids as pollen-vectors in more detail, considering their specialisation
104 in terms of the pollen they transport and their interaction evenness within plant communities;
105 3) To compare the abundance and diversity of syrphids and non-syrphid Diptera in
106 agricultural habitats. 4) To estimate the relative amount of pollen transported by Syrphidae
107 and non-syrphid dipteran communities in agricultural habitats.

108

109 **Methods**

110

111 Our analysis incorporated data from 11 independent projects comprising a total of 71 plant-
112 pollinator-visitation networks and 30 pollen-transport networks (Table S1-supplementary
113 material). Together these characterize the interactions between 9082 flower-visitors (520
114 species) and 261 plant species. The visitation networks quantified which insect species
115 visited which plant species and the pollen-transport networks quantified the number and
116 identity of pollen-grains on the insects' bodies. Few studies have collected quantitative
117 pollen-load data at the community-level, therefore this study is limited to the studies cited in
118 Table S1. The data were gathered using a standard methodology, this reducing the variation
119 between studies. We concentrate on temperate ecosystems within the UK (with the exception
120 of 1 Australian study) as dictated by the available data; although the datasets originate from a
121 range of habitats (Table S1) most are from farmland.

122

123 We collated the network data into four datasets. The first dataset comprised 18 pollen-
124 transport networks from five projects providing pollen-load data at the individual-level (3717
125 pollinators; 404 pollinator species and 61 plant species) (Objectives 1 and 2). The second
126 dataset comprised 30 independent pollen-transport networks from eight projects (450
127 pollinator species and 230 plant species) providing pollen-load data at the pollinator species-
128 level (Objective 2). The third dataset consisted of 71 visitation networks from all 11 studies
129 (Objective 2). The fourth dataset comprised visitation data from 33 independent farms from
130 six agricultural projects (Objectives 3 and 4).

131

132 Objective 1. Pollen-loads of flower-visiting insect taxa

133

134 The median count of pollen grains per individual insect was calculated for each species of the
135 Hymenoptera, Coleoptera, Diptera and Lepidoptera for each of the 18 networks. Some Orders
136 were sub-divided, resulting in nine groups: Hymenoptera were subdivided into pollinator
137 groups; honey bees (*Apis mellifera*), bumbles bees (*Bombus* sp.) and solitary bees and Diptera
138 were divided into the Syrphidae and non-syrphid Diptera. A general linear mixed effects
139 model (GLMM) (package: lme4 [37]) in R Statistical Environment fitted with normal errors
140 and identity link was used to determine the difference in pollen-loads i.e. pollen-grain count
141 (response variable- log_e transformed) between the different taxa (fixed factor). Post-hoc
142 Tukey tests (package: multcomp) [38] were used.

143

144 Four additional variables were included in the model to account for additional sources of
145 variation: ‘Habitat’, ‘Location’, ‘Sampling’ and ‘Study’. Random factors were used in the
146 analyses except where the number of levels <5, where fixed effects were used instead [39]

147 (Table S1 and S2 for details of GLMMs). Conditional R^2 (variance explained by both fixed
148 and random factors) and marginal R^2 (variance explained by fixed factors) are reported.

149

150 Objective 2. Specialisation and interaction evenness of the dipteran groups

151

152 Syrphidae and non-syrphid species' interaction specialisation with the lower trophic level
153 (specialisation relating to pollen species carried), was assessed using the 'd' statistic
154 (package 'bipartite') [40] within each of the 30 pollen-transport networks. Measures of 'd'
155 range from 0 (no specialisation) to 1 (perfect specialist). Differences in pollen specialisation
156 were determined by a GLMM (normal errors, identity link).

157

158 We also compared interaction evenness (Shannon's evenness; a measure of the equitability of
159 visits between visitors and their interacting species [41]) between syrphid (n=1923) and non-
160 syrphid Diptera (n=4776) visitation networks (package 'bipartite'). Interaction evenness
161 equals 1 when the plant-pollinator interactions are uniformly distributed between species.
162 Separate matrices were created for the Syrphidae and non-Syrphid Diptera from each
163 visitation network (species-level visitation data) and evenness calculated per network.
164 Differences in interaction evenness between the syrphid and non-syrphid Diptera were
165 determined by a GLMM (normal errors, identity link).

166

167 Objective 3. The abundance and diversity of syrphid and non-syrphid Diptera in farmland

168

169 Data from 33 independent farms from six studies were used to compare the abundance (count
170 of insects) and species richness (count of species) per farm (response variables) of the syrphid
171 and non-syrphid Diptera (fixed factors) utilizing GLMMs (Poisson errors). An observation-

172 level random effect was added to both models to create a Poisson-lognormal model
173 accounting for overdispersion [42]. As species richness is likely to increase with the number
174 of individuals captured we performed a rarefaction analysis to standardise for variable
175 network sizes. Rarefaction allowed the calculation of species richness for a given number of
176 individual samples [43] and was calculated using the vegan package in R. Species richness
177 estimates were compared with a GLMM (normal errors, identity link). GLMMs for Objective
178 3 and 4 included 'farm' as an additional random factor.

179

180 Objective 4. Pollen transported by the syrphid and non-syrphid dipteran communities in 181 farmland.

182

183 Pollen-load data were available for three out of the six studies based in agricultural habitats.
184 Therefore to estimate the relative pollen-carrying capacity of the syrphid and non-syrphid
185 dipteran communities we: 1) calculated the median pollen-loads per individual of syrphid
186 (n=583) and non-syrphid Diptera (n=632) from the three farm studies; 2) we then multiplied
187 these values by the abundance of each dipteran group for each of the 33 farm datasets.
188 Differences between the two groups were investigated using a GLMM (Poisson errors with
189 an observation-level random effect).

190

191 **Results**

192

193 Objective 1. Pollen-loads of flower-visiting insect taxa

194

195 There was a significant difference in pollen-loads between the flower-visitor taxa ($\chi^2=$
196 104.18, d.f.=8, $p<0.001$, $R^2m=0.48$, $R^2c=0.53$ [44], Figure 1, Table S2). The Hymenoptera

197 carried the largest pollen-loads; but within this taxon there was no significant difference
198 between the bumble bees, solitary bees and honey bees (Figure 1). Within the Diptera, there
199 was no significant difference between the Syrphidae and non-syrphid Diptera (Figure 1). The
200 pollen-loads of the Syrphidae did not differ significantly from the honey bees; however the
201 Syrphidae had significantly lower pollen-loads than the other hymenopteran sub-groups. The
202 non-syrphid Diptera had lower pollen-loads than all the hymenopteran sub-groups (Figure 1).
203 The Coleoptera and Lepidoptera had significantly lower pollen-loads than all hymenopteran
204 groups, but did not differ significantly from each other (Figure 1). With the exception of the
205 Lepidoptera having lower pollen-loads than the Syrphidae, these two groups did not differ
206 from the Dipteran groups (Figure 1).

207

208 Objective 2. Specialisation and interaction evenness of the dipteran groups

209

210 The Syrphidae and non-syrphid Diptera did not differ in specialisation (0.24 and 0.21
211 respectively) in the pollen-transport networks ($\chi^2=3.07$, d.f.=1, $p=0.080$, $R^2m=0.26$,
212 $R^2c=0.65$, Table S2). The Syrphidae had significantly higher interaction evenness (0.65) in
213 the visitation networks than the non-syrphid Diptera (0.61) ($\chi^2=10.65$, d.f.=1, $p=0.001$,
214 $R^2m=0.38$, $R^2c=0.91$, Table S2).

215

216 Objective 3. The abundance and diversity of syrphid and non-syrphid Diptera in farmland

217

218 Non-syrphid Diptera were significantly more abundant than the Syrphidae in agricultural
219 habitats; a median of 28 and 6 insects were recorded per farm respectively ($\chi^2=24.29$, d.f.=1,
220 $p<0.001$, $R^2m=0.21$, $R^2c=0.83$, Figure 2, Table S2). On average the non-syrphid Diptera
221 made up 82% (s=23%) of the dipteran abundance recorded on the farms. Species richness of

222 non-syrphid Diptera was also higher than the Syrphidae; a median of 7 and 3 species per farm
223 respectively ($\chi^2=27.08$, d.f.=1, $p<0.001$, $R^2m=0.15$, $R^2c=0.88$, Figure 2, Table S2) (Figure 2).
224 On average non-syrphid Diptera made up 73% (s=19%) of dipteran species. Following
225 rarefaction the species richness of the non-syrphid Diptera was still greater than the
226 Syrphidae ($\chi^2=23.27$, d.f.=1, $p<0.001$, $R^2m=0.055$, $R^2c=0.94$); therefore patterns detected
227 were unlikely to be driven by sampling effects. Together the dipteran groups made up 67% of
228 the total abundance and 66% of the total species richness of all flower-visitors in the farm
229 networks.

230

231 Objective 4. Pollen transported by the syrphid and non-syrphid dipteran communities in
232 farmland.

233

234 Median pollen-load for the Syrphidae and non-syrphid Diptera in the agricultural habitats was
235 7 and 16 pollen grains respectively; this was multiplied by dipteran abundance counted in
236 each of the farms. The non-syrphid Diptera communities carried significantly more pollen
237 than the Syrphidae ($\chi^2=43.79$, d.f.=1, $p<0.001$, $R^2m=0.33$, $R^2c=0.80$, Table S2); 84% of all
238 dipteran-carried pollen was carried by the non-syrphid Diptera.

239

240 Discussion

241

242 To our knowledge this is the first study to highlight the potential importance of non-syrphid
243 Diptera as pollinators using a network approach at a multi-family, multi-habitat level. The
244 syrphid and non-syrphid Diptera did not significantly differ in their pollen-loads. There was
245 no difference in pollen-transport specialisation between the two groups. However, the
246 Syrphidae had significantly greater visitation evenness in the visitation networks. The non-

247 syrphid Diptera made up the majority of the flower-visiting Diptera in agricultural habitats
248 and we estimate that they carry 84% of total pollen carried by farmland Diptera.

249

250 Our study is however limited to temperate ecosystems (predominantly UK farmland) due to
251 the availability of data, consequently the results should be considered in this context only. If
252 tropical systems were included it's possible that different conclusions would be drawn as
253 multi-latitudinal studies on plant-pollinator networks have revealed differences in network
254 structure between temperate and tropical climates e.g. specialisation [45].

255

256 The pollen-loads of the different flower-visiting taxa

257

258 As predicted, the Hymenoptera carried the highest pollen-loads. Bees make many visits to
259 flowers to provision their broods, and many have specialized structures for pollen transport
260 [27]. Although bees are acknowledged to be highly effective pollinators [46] many species
261 are in decline. Most widely reported are honeybee populations; primarily a result of heavy
262 pathogen and parasite loads, pesticide use and diminishing resources [5, 6, 47]. Declines have
263 also been observed for many wild pollinator species, though this rate of decline has slowed or
264 reversed for several species [3, 5, 6]. Ecological conditions and anthropogenic pressures
265 affecting bees may differ from those affecting flies due to the differences in their ecology
266 [48] and it is possible that these alternative pollinator taxa could provide some insurance
267 against bee losses. Many families of Diptera, including the Muscidae and Scathophagidae,
268 have bristles which trap pollen; the Bombyliidae are furry; and the Acroceridae are thought to
269 have hairs adapted for carrying pollen [7]. Indeed, the average pollen-load of the Diptera was
270 second to that of the Hymenoptera, this being in agreement to the findings of Rader *et al.* [36]
271 where Apidae generally carried higher pollen-loads than dipteran taxa. In the current study

272 the Syrphidae pollen-loads did not significantly differ from *Apis*, this strongly suggesting that
273 Dipteran groups could be important as pollinators.

274

275 The ‘insurance value’ of Diptera is conditional on the fly populations having similar
276 functional attributes (e.g. mouth parts, feeding behaviour and phenology) to fill the niche of
277 declining bee species. Bombyliidae flies have long tongues which can pollinate flowers
278 possessing long-tube corollas; however the presence of this group in our dataset was low (just
279 13 individuals). Ideally functional diversity analyses should be performed in order to
280 determine if Diptera could compensate for bee declines. Unfortunately though, trait data for
281 many dipteran species is currently lacking, in part because their importance as pollinators is
282 often overlooked.

283

284 The syrphid and non-syrphid Diptera as potential pollinators

285

286 Pollen-loads (number of grains) did not differ significantly between the syrphid and non-
287 syrphid Diptera. As an insect’s pollen-load influences the likelihood of pollen being
288 transferred to stigmas [34, 35], the syrphids and non-syrphids may not differ in their efficacy
289 as pollinators. Thus, it may be premature to dismiss the non-syrphid Diptera in pollination
290 studies on the grounds that, unlike the Syrphidae, they are unimportant. That said further
291 research, especially to measure seed-set following visits by specific taxa, is required to
292 confirm this. Indeed, a limitation of our approach is our focus on the visitation and pollen-
293 transport stages of the pollination process. The most comprehensive way of assessing
294 pollinator importance would be to assess their relative influences on seed-set. This would
295 require bagging of replicate flowers after single visits by each flower-visiting species; a
296 challenging approach at the community level.

297

298 There was no difference in specialisation of the non-syrphid Diptera and the Syrphidae in
299 terms of the identity of pollen transported. Pollen specialisation has implications for the
300 pollination of plant communities. More generalised pollen transfer gives the potential to
301 pollinate a greater diversity of species, although pollination may be less effective [49]. The
302 Syrphidae had greater interaction evenness and this has potential implications for the overall
303 stability of the plant-pollinator community; higher interaction evenness is associated with
304 stability [50].

305

306 Non-syrphid dipteran abundance and diversity in agro-ecosystems.

307

308 The greater richness of the non-syrphid Diptera found in agro-ecosystems could provide a
309 more stable pollination service as richness is positively associated with the stability of
310 ecosystem processes [51, 52]. We estimated that the non-syrphid Diptera carried 84% of the
311 dipteran pollen in farmland habitats. Considering Diptera made up 67% of all flower-visitor
312 abundance in the farm networks this is a significant proportion of the pollen transported in
313 farmland. Unlike many bee species, the non-syrphid Diptera have not been widely reported to
314 be threatened by current agricultural practices, although it is possible that any declines have
315 been overlooked and further studies are needed to assess their vulnerability.

316

317 Conclusion

318

319 Our analysis of pollen-transport and visitation networks strongly suggests that it is
320 inappropriate to exclude non-syrphid Diptera from pollination studies. Looking forward, our
321 assessment of pollinator importance sensu Herrera [31] needs to be augmented in the future

322 with pollen-transfer and ultimately seed-set analyses using controlled experiments. Per-visit
323 effectiveness of non-syrphid dipteran species for crops and wild plants should be assessed
324 focusing on families that may fill the niche of declining bees such as the Bombyllidae. More
325 generally, training in dipteran taxonomy should be more available to ecologists. Alternatively
326 specialist taxonomists should be included in research projects to prevent pollination
327 biologists being deterred from recording Diptera due to identification difficulties. Given the
328 current declines in Hymenoptera along with large unknowns such as the effect of climate
329 change on pollinators, improving our understanding of the role of the less well-known
330 pollinator groups is timely.

331

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335

336 Data accessibility

337 The data used in this paper can be accessed via Dryad: doi:10.5061/dryad.41m4d

338

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525 Figure Legends

526

527 **Figure 1.** Means (\pm standard deviations) of the \log_e -transformed pollen load data (count of
528 pollen grains per individual insect) analysed for Objective 1: Hymenoptera (n=2201)
529 (separated into *Bombus* (n=901), *Apis* (n=1138) and solitary bees (n=115)), Diptera (n=998)
530 (separated into the Syrphidae (n=609) and non-syrphid Diptera (n=389)), Coleoptera (n=447)
531 and Lepidoptera (n=71) across 18 pollen-transport networks. Pollinator groups with shared
532 letters have no significant difference in pollen-loads.

533

534 **Figure 2.** Absolute differences in: a) total abundance and b) species richness between the
535 Syrphidae and non-syrphid Diptera found on each of the 33 farms (each bar represents a
536 farm). Positive values show higher abundance or species richness of the non-syrphid Diptera
537 than the Syrphidae.

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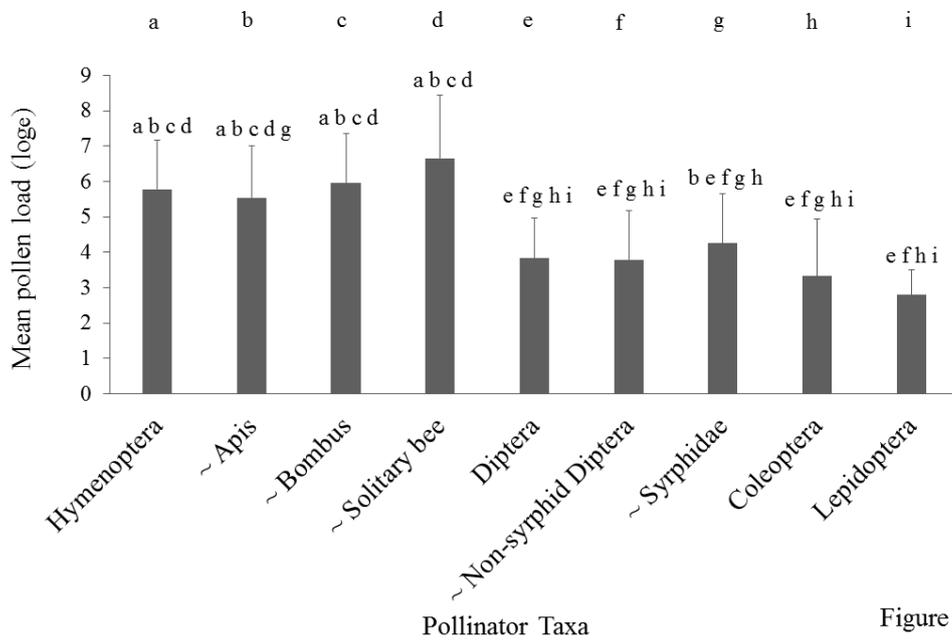
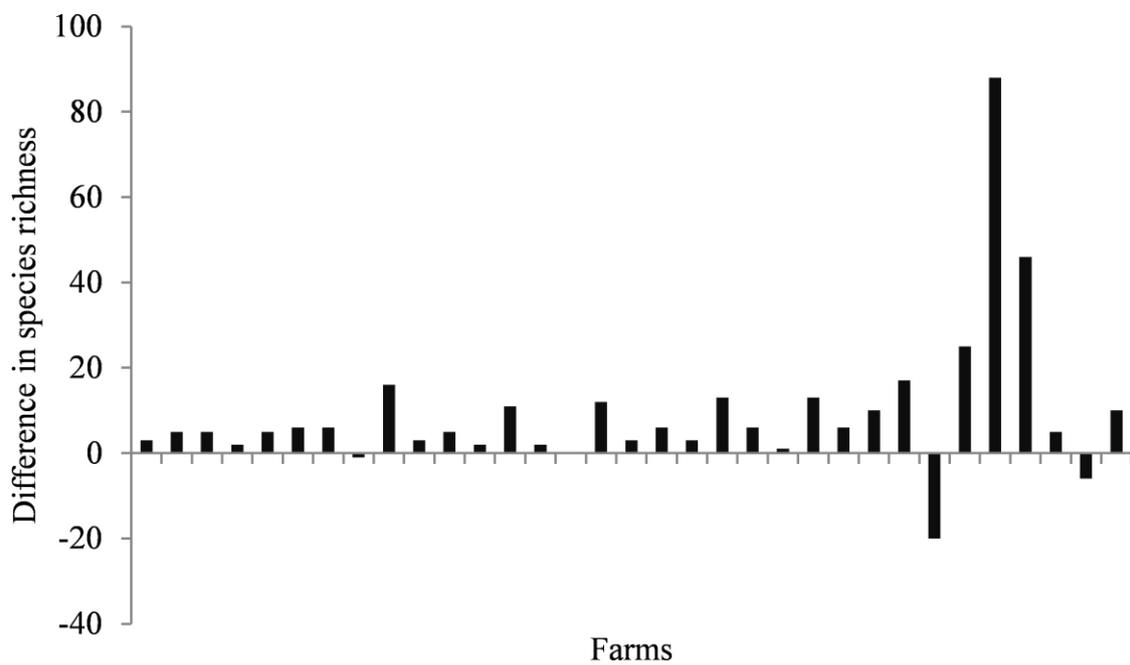
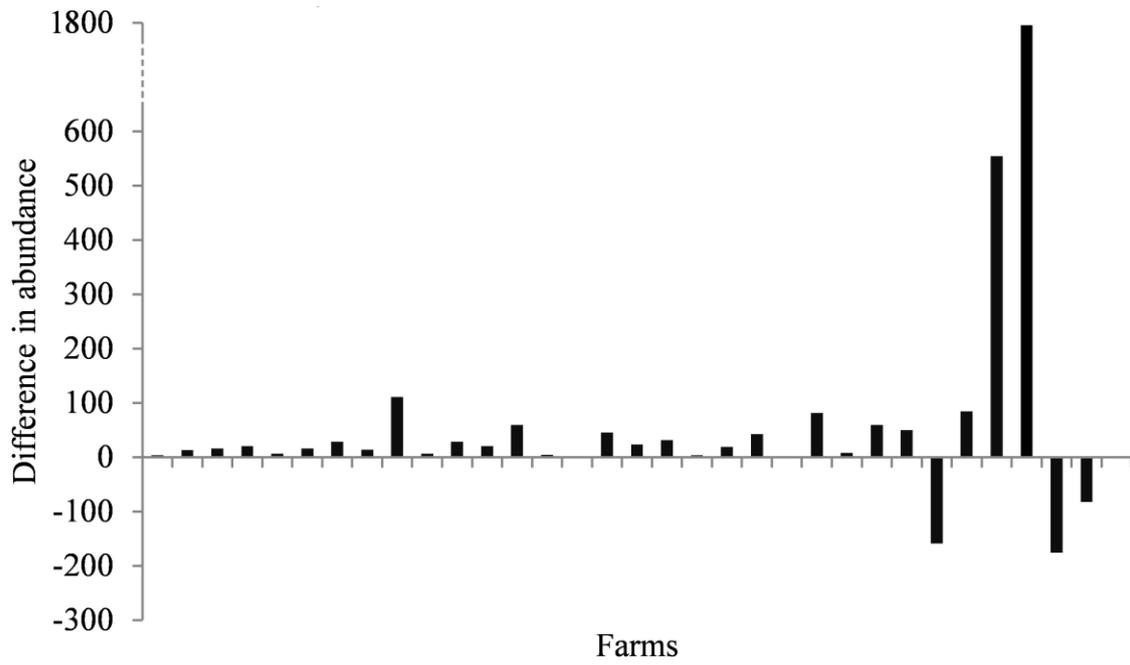


Figure 1

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Figure 1

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Figure 2

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