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Diverse pollinator communities enhance plant reproductive success

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Abstract: Understanding the functional consequences of biodiversity loss is a major goal of ecology. Animal-mediated pollination is an essential ecosystem function and service provided to mankind. However, little is known how pollinator diversity could affect pollination services. Using a substitutive design, we experimentally manipulated functional group (FG) and species richness of pollinator communities to investigate their consequences on the reproductive success of an obligate out-crossing model plant species, *Raphanus sativus*. Both fruit and seed set increased with pollinator FG richness. Furthermore, seed set increased with species richness in pollinator communities composed of a single FG. However, in multiple-FG communities, highest species richness resulted in slightly reduced pollination services compared with intermediate species richness. Our analysis indicates that the presence of social bees, which showed roughly four times higher visitation rates than solitary bees or hoverflies, was an important factor contributing to the positive pollinator diversity–pollination service relationship, in particular, for fruit set. Visitation rate at different daytimes, and less so among flower heights, varied among social bees, solitary bees and hoverflies, indicating a niche complementarity among these pollinator groups. Our study demonstrates enhanced pollination services of diverse pollinator communities at the plant population level and suggests that both the niche complementarity and the presence of specific taxa in a pollinator community drive this positive relationship.

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1 Running title: Functional consequences of pollinator diversity

2

3 **Diverse pollinator communities enhance plant reproductive success**

4

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18 Summary

19 Understanding the functional consequences of biodiversity loss is a major goal of ecology.
20 Animal-mediated pollination is an essential ecosystem function and service provided to
21 humankind. However, little is known how pollinator diversity could affect pollination
22 services. Using a substitutive design we experimentally manipulated functional group and
23 species richness of pollinator communities to investigate their consequences on the
24 reproductive success of an obligate out-crossing model plant species, *Raphanus sativus*. Both
25 fruit and seed set increased with pollinator functional group richness. Furthermore, seed set
26 increased with species richness in pollinator communities composed of a single functional
27 group. However, in multiple-functional group communities, highest species richness resulted
28 in slightly reduced pollination services compared to intermediate species richness. Our
29 analysis indicates that the presence of social bees, which showed roughly four times higher
30 visitation rates than solitary bees or hoverflies, was an important factor contributing to the
31 positive pollinator diversity–pollination service relationship, in particular for fruit set.
32 Daytime and less so height of flower visits varied among social bees, solitary bees and
33 hoverflies, indicating niche complementarity among these pollinator groups. Our study
34 demonstrates enhanced pollination services of diverse pollinator communities at the plant
35 population level and suggests that both niche complementarity and the presence of specific
36 taxa in a pollinator community drive this positive relationship.

37

38 Key words

39 Biodiversity–ecosystem function relationship, complementary resource use, ecosystem
40 services, plant–pollinator interactions, social bees, solitary bees, hoverflies

41 Introduction

42 Understanding the consequences of biodiversity loss on ecosystem functioning and services
43 has developed into a central theme in ecology [1–3]. Animal pollination is a critical
44 ecosystem service as most angiosperms are pollen limited [4] and rely on animals for sexual
45 reproduction [5]. A large proportion of the human diet depends directly or indirectly on
46 animal pollination [6]. However, there is evidence that pollinators are declining in many parts
47 of the world as a consequence of environmental degradation [7–9]. Recent research has linked
48 reductions in the pollination of crops and wild plants in intensively managed agro-ecosystems
49 to declines in density and diversity of pollinators [10–18]. However, in these observational
50 studies, aggregate abundance and diversity of pollinators are correlated. Thus, an
51 experimental approach controlling for the confounding effect of aggregate abundance is
52 needed in order to gain a better and more mechanistic understanding of the role of pollinator
53 diversity in the provisioning of pollination services [19–21, see also 22].

54 Mainly three mechanisms have been proposed to explain positive pollinator diversity–
55 pollination service relationships [20]: first, such relationships may result from a positive
56 sampling [23, 24] or selection effect [25], by which diverse communities are more likely to
57 include functionally highly effective species or species groups. Pollination effectiveness
58 among pollinator groups can vary in the quality of the pollen transfer as a consequence of
59 morphological and behavioural differences, but primarily due to variation in flower visitation
60 rates [26]. Second, under functional facilitation some community members enhance the
61 functional performance of others [27]. For example, honey bees switched more often between
62 plant individuals of sunflower hybrids in the presence of foraging wild bees, thereby
63 facilitating cross-pollination [28]. Third, functional complementarity through niche
64 partitioning [29] in the flower visitation patterns of pollinators may lead to enhanced
65 pollination services provided by diverse pollinator communities [16, 19, 21]. Such niche
66 partitioning may occur at multiple temporal and spatial scales [21]. At a large scale, inter-

67 annual [18] or regional complementarity may enhance pollination services and their stability.
68 Furthermore, diversity effects in pollination may be due to a diverse plant community being
69 pollinated (corresponding to resource heterogeneity) [19] or to differences among pollinators
70 visiting a single plant species [21, 30]. The latter can occur, for example, when different
71 species in a pollinator community partition their foraging activities during different daytimes
72 [31] or among flowers at different positions within plant individuals [16]. However,
73 experimental knowledge of the functional consequences of pollinator niche partitioning in
74 diverse pollinator communities for the pollination success of single plant species is currently
75 lacking [but see 22].

76 In the present study we experimentally manipulated functional group richness (one vs.
77 three functional groups) and species richness (one, three and nine species) of caged pollinator
78 communities in a substitutive design and analyzed patterns of pollinator visitation to the
79 single plant *Raphanus sativus* L. as a model species to address the following questions: (1)
80 How does the presence and richness of pollinator species and functional groups affect fruit
81 and seed set of a self-incompatible, insect-pollinated plant species? (2) Do single functional
82 groups and communities of pollinators differ in their temporal (diurnal) and spatial (flower
83 visitation height) niches?

84

85 **Material and Methods**

86 *Study plant species*

87 Radish, *Raphanus sativus* ssp. *oleiformes* L. (Brassicaceae), is a hermaphroditic, annual herb
88 native to Europe. It produces up to several hundred flowers per plant and is visited by a wide
89 variety of flower visitors, including solitary and social bees, hoverflies and butterflies (e.g.
90 [13, 26, 32]). *Raphanus sativus* has a sporophytic self-incompatibility system and relies on
91 animal pollination for reproduction [33]. Thus, *R. sativus* is an ideal model species to study
92 the effects of diverse pollinator communities on life-time plant reproductive success [13, 26].

93

94 *Experimental design*

95 For the pollination treatments twelve cubic cages (side length 2 m, mesh width 0.8 mm [19])
96 were set up in spring 2007 in the experimental garden of the University of Zurich
97 (Switzerland). The cages prevented natural pollination of the experimental plant populations
98 and a ground-covering plastic foil prevented natural plant establishment inside cages. During
99 a pollination treatment a cage contained nine potted, abundantly flowering plants of *R. sativus*
100 arranged in a grid with a width of 50 cm between plants. During spring 2007 *R. sativus* had
101 been sown directly into these pots containing 5 L of standardized, nutrient-rich garden soil
102 and grown in a pollinator-free glasshouse. To ensure that flowering plants of roughly the same
103 age and size were available for the pollination treatments they were sown at four different
104 dates with a time-lag of roughly one week. Plants were randomly distributed among cages
105 three to four days prior to a pollination treatment.

106 Pollinator species richness during the pollination treatments (1, 3 and 9 species) and
107 pollinator functional group richness (1 vs. 3 groups) were manipulated in a substitutive design
108 (Fig. 1) with a constant number of 18 pollinator individuals per community (including single-
109 species communities). In preliminary experiments we had identified this level of aggregate
110 pollinator abundance to result in visitation rates very similar to those reported for radish under
111 natural conditions (e.g. [32, 34]; M. Albrecht, unpublished data). The 3-species communities
112 were not overlapping and included either 3 species of a single functional group or one species
113 of each of the 3 functional groups (Fig. 1). The 3 functional groups used in the experiment
114 were defined *a priori* as social bees (eusocial, large bees), solitary bees (solitary and
115 primitively eusocial, smaller bees) and hoverflies. These three groups are generally
116 considered the most important pollinator functional groups in Europe, based on differences in
117 foraging behaviour and morphology (e.g. [11, 17, 19] and references therein). They represent
118 the main functional groups pollinating radish [13, 32, 34], although butterflies can also be

119 functionally important in some regions and ecosystems [26]. Each functional group comprised
120 3 species, thus pollinator communities of up to 9 species were used in the experiment: the
121 social bee species *Bombus terrestris* L. (A₁), *Bombus pascuorum* Scopoli (A₂) and *Apis*
122 *mellifera* L. (A₃); the solitary bee species *Halictus rubicundus* Christ (B₁), *Andrena flavipes*
123 Panzer (B₂), *Lasioglossum* sp. (B₃); and the hoverfly species *Eristalis tenax* Latreille (C₁),
124 *Episyrphus balteatus* De Geer (C₂) and *Sphaerophoria* sp. (C₃) (Fig. 1). The *Lasioglossum*
125 bees were most likely all *L. morio* Fabricius and the *Sphaerophoria* hoverflies most likely all
126 *S. scripta* L., but we cannot totally rule out the possibility that also some individuals of
127 morphologically very similar congeneric species were collected as identification of these
128 species can be difficult. All species are highly generalised, polylectic flower visitors [35, 36].
129 The 9-species community was replicated six times, whereas each unique 1- and 3-species
130 community was replicated twice (except the single-species “community” of *H. rubicundus*,
131 which could not be replicated due to the low number of individuals of this species available
132 for the experiment).

133

134 *Pollination rounds*

135 The experiment was conducted during four days (four time blocks, hereafter “pollination
136 rounds”) on 17 July, 25 July, 1 August and 9 August 2007 under sunny weather conditions. A
137 one-day period for each pollination round was used because flowers of *R. sativus* are open and
138 receptive for roughly one day, with most ovules available for fertilization for a few hours
139 [37]. Most pollinator species were captured at different locations in the northeast of
140 Switzerland. Individuals of the hoverfly species *Episyrphus balteatus* were purchased as
141 pupae from Katz Biotech AG, Germany. Two large colonies of *Bombus terrestris* were
142 purchased from Leu & Gygax AG, Switzerland. For each community comprising *B. terrestris*
143 half of the individuals required for a certain pollinator treatment were taken from colony 1
144 and the other half from colony 2. Pollinators (both purchased and captured individuals) were

145 kept in boxes (acryl-glass and fine-meshed fabric; 50 x 50 x 150 cm) in a climate chamber
146 (20° C, 60% humidity) and were fed with sugar- and honey-water and finely ground pollen
147 (Leu & Gygax AG) until the day before using them for a pollination round. For each
148 pollination round, pollinators were introduced into cages at 8 h and removed at 19 h on the
149 same day. Immediately after a pollination round, stalks of open, not wilted flowers of each *R.*
150 *sativus* plant were marked with a permanent marker. The next day, potted plants were brought
151 back to the pollinator-free glasshouse until fruit collection. Seed set and fruit set was
152 determined as the number of seeds and number of fruits set, respectively, per marked flower.

153

154 *Pollinator observations*

155 To investigate possible mechanisms of pollinator-mediated consequences on plant
156 reproduction, the number of visits — and the identity of the pollinator species performing the
157 visit — was recorded for a randomly selected focal plant for each pollinator community
158 treatment. Observations were made during each of the four pollination rounds. No
159 observations were made before 9 h to ensure that pollinators had enough time to calm down
160 after introduction into cages. Bees needed approximately 30 min to calm down before starting
161 to visit flowers, while hoverflies usually started to visit flowers immediately (M. Albrecht,
162 personal observation; in agreement with observation by Fontaine *et al.* [19]). For each visit
163 the height of the flower visited by a pollinator was estimated and assigned to one of three
164 flower height classes (basal [< 40 cm]; medium [40–80 cm]; apical [> 80 cm]). Observations
165 of pollinator communities were done during 30-min observation periods during each of four
166 different daytime periods: 9.00–11.30, 11.30–14.00, 14.00–16.30 and 16.30–19.00. Despite
167 extensive observations (3660 min of total observation time) and several people observing
168 simultaneously during pollination rounds, it was not possible to observe all replicates of the
169 different pollinator communities, and the 3-species community $A_2B_2C_2$ was not observed.

170

171 *Data analysis*

172 Linear mixed-effects models were fitted using the lme-function of the nlme package supplied
173 in the R-system of statistical computing (R Development Core Team 2009). A model
174 selection procedure based on Akaike's Information Criterion (AIC) was used to select the
175 most adequate model, using maximum likelihood for model comparisons and backward
176 selection starting from the full model [38]. Most adequate models were fitted with restricted
177 maximum likelihood and model fit was assessed by testing the residuals for normality and
178 homoscedasticity and by plotting the residuals against the predicted values. Means \pm 1 SE are
179 reported. The relative importance of the predictor variables of the full model was calculated as
180 the proportion of the total variance explained by each variable using increments of multiple R
181 squared (i.e. percentage Typ 1 Sum of Squares) of the fixed model versions of the fitted linear
182 mixed models [39]. The calculated percentages can be used as measures of effect sizes [39].

183 To test the effect of pollinator functional group richness, species richness (and their
184 interaction) and the presence of functional groups on the response variables fruit and seed set,
185 they were included as fixed effects in the full model. Species richness was log-transformed
186 because this gave a better fit than linear species richness. However, we also calculated models
187 in which species richness was fitted with a 2nd degree polynomial (i.e. [linear species richness]
188 + [linear species richness]²) to test for a hump-shaped relationship (results not shown). Cage
189 (nested within pollination round) and community composition were included as random
190 effects. Because this analysis indicated that species richness did not explain much variation
191 when fitted after functional group richness (see Results section), we focused on functional
192 group identity and richness as explanatory variables in the subsequent analysis of niche
193 complementarity. The full model, fitted to test whether spatio-temporal resource use (square-
194 root transformed number of visited flowers) differed among pollinator functional groups,
195 contained the fixed factors pollinator functional group identity, daytime (four daytime
196 periods) and flower height (three height classes), and all their possible interactions, and

197 pollinator species identity, cage and pollination round as random effects. To analyse
198 visitation-rate patterns of whole pollinator communities, the same model but with the fixed
199 effect functional group richness instead of functional group identity and the random effect
200 pollinator community identity instead of pollinator species identity was fitted.

201

202 **Results**

203 *What are the functional consequences of pollinator richness?*

204 Functional group richness of pollinators increased plant seed set ($F_{1,27} = 9.60$, $P = 0.005$; 1
205 FG: 2.91 ± 0.17 , 3 FGs: 3.48 ± 0.28 ; Fig. 2a), explaining 55% of the total variation due to the
206 fixed effects of the full model. However, log(species richness) only explained an additional
207 non-significant amount of 9% (fitted after functional group richness in the full model; $F_{1,27} =$
208 1.45 , $P = 0.239$; Fig. 2a). The presence or absence of social bees explained an additional
209 marginally significant amount of 19% (fitted after functional group richness and log(species
210 richness); $F_{1,27} = 3.19$, $P = 0.085$). Furthermore, there was no significant interaction between
211 functional group richness and log(species richness) (fitted after functional group richness,
212 log(species richness) and presence of social bees; $F_{1,27} = 1.44$, $P = 0.241$).

213 Functional group richness of pollinators also increased plant fruit set ($F_{1,26} = 10.86$, P
214 $= 0.003$; 1 FG: 0.61 ± 0.04 , 3 FGs: 0.78 ± 0.04 ; Fig. 2b), explaining 37% of the total variation
215 due to the fixed effects of the full model. Similar to seed set, the positive effect of log(species
216 richness) on fruit set only explained an additional non-significant amount of 2% (fitted after
217 functional group richness in the full model; $F_{1,26} = 0.94$, $P = 0.342$; Fig. 2b). Most of the total
218 variation in fruit set due to fixed effects, namely 60%, were explained by the presence or
219 absence of social bees (fitted after functional group richness and log(species richness); $F_{1,26} =$
220 19.66 , $P < 0.001$). The interaction between functional group richness and log(species
221 richness) was very small and not significant (fitted after functional group richness, log(species
222 richness) and presence of social bees; $F_{1,27} = 1.44$, $P = 0.241$). The most adequate model for

223 fruit set contained social bee presence (present: 0.78 ± 0.04 , absent: 0.52 ± 0.04) as the only
224 fixed explanatory variable.

225

226 *Do pollinator functional groups differ in spatio-temporal flower visitation?*

227 Pollinator functional groups tended to differ in the number of flowers visited ($F_{2,6} = 4.86$, $P =$
228 0.055), which was primarily a result of the roughly four times higher visitation rate of social
229 bees compared to solitary bees or hoverflies (Fig. 3). The three functional groups differed in
230 their flower-visitation patterns during the day, irrespective of whether only communities
231 consisting of a single functional group were analysed (functional group \times daytime interaction:
232 $F_{6,87} = 4.81$, $P < 0.001$) or also three-functional-group communities were included in the
233 analysis ($F_{6,229} = 3.21$, $P = 0.005$; Fig. 3). However, when only the communities consisting of
234 three functional groups were analysed, the three functional groups did not significantly differ
235 in flower visitation among the four different daytime periods ($F_{6,108} = 0.92$, $P = 0.484$), but
236 social bees still tended to differ from solitary bees and hoverflies in visitation rate early
237 (morning and noon) compared to later during the day (afternoon and evening; $F_{1,115} = 3.82$, P
238 $= 0.053$). Social bees visited most flowers between 14.00 and 16.30 h, in contrast to solitary
239 bees, visiting most flowers in the morning hours between 9.00 and 11.30 h, while hover flies
240 visited most flowers in the morning and noon, with similar numbers recorded between 9 and
241 11.30 and between 11.30 and 14 h, respectively (Fig. 3). The three functional groups did not
242 differ in the relative number of visits to flowers at lower parts of plants compared to more
243 upper parts when single and three functional-group communities were analysed separately,
244 although there was a trend for social bees to visit a relatively higher number of basal flowers
245 when all communities were analysed (interaction functional group \times flower height contrast
246 [basal vs. medium and apical]: $F_{2,69} = 2.56$, $P = 0.085$). While including the functional group
247 \times daytime interaction (indicating diurnal visitation differences among pollinator groups)
248 substantially enhanced the model fit (Δ AIC 7.18; all communities included), including the

249 functional group \times flower height interaction only slightly increased model performance (Δ
250 AIC < 2), confirming that diurnal differences in visitation rates among functional groups
251 played a more important role than spatial differences (visits to flowers at different heights).

252

253 *Do pollinator communities differ in spatio-temporal flower visitation?*

254 Analysing visitation rates of whole communities, the average number of visited flowers
255 increased with functional group richness from 14.4 (\pm 3.4) to 22.7 (\pm 6.9) visits per plant
256 during 30 min, but this increase was statistically not significant ($F_{1,13} = 1.17$, $P = 0.299$).

257 However, visitation rate was significantly increased in communities including the functional
258 group social bees (present: 25.4 \pm 3.1, absent: 7.9 \pm 2.8; $F_{1,13} = 13.63$, $P = 0.003$). Moreover,
259 the number of flowers a pollinator community visited varied among different daytimes:

260 visitation rate was highest during noon and afternoon (11.30–14.00: 19.3 \pm 3.3; 14.00–16.30:

261 17.1 \pm 3.2), somewhat lower in the morning (9.00–11.30: 14.2 \pm 1.8) and lowest in the

262 evening (16.30–18.00: 10.4 \pm 2.4). The number of visited flowers tended also to be influenced

263 by the position of the flowers within the plant: 22.3 (\pm 2.8) visits per 30 min to flowers at a

264 height of 40–80 cm, 17.2 (\pm 2.5) visits to flowers > 80 cm and 7.1 (\pm 1.2) visits to flowers <

265 40 cm. Furthermore, daytime visitation was contingent on whether it included social bees or

266 not (social bee presence in community \times daytime interaction: $F_{3,111} = 8.24$, $P < 0.001$):

267 visitation rate of communities containing social bees was roughly twice as high during noon

268 and afternoon (31.3 \pm 5.3 and 34.1 \pm 5.0, respectively) than during morning (9.00–11.30: 17.9

269 \pm 3.3) and evening (16.30–18.00: 17.0 \pm 4.7), while visitation rate in communities without

270 social bees was highest in the morning (9.00–11.30: 11.9 \pm 2.0; 11.30–14.00: 8.7 \pm 3.1;

271 14.00–16.30: 6.5 \pm 1.8; 16.30–18.00: 5.0 \pm 1.6). The most adequate model explaining

272 variation in flower visitation by the entire pollinator community contained the fixed effect

273 social bee presence in the community, daytime and flower height and the interactions of the

274 latter two with social bee presence.

275

276 **Discussion**277 *What are the functional consequences of pollinator diversity?*

278 Our study demonstrates enhanced population-level reproductive success of an insect-
279 pollinated model species, *Raphanus sativus*, as a consequence of increased pollination
280 services provided by a higher functional richness of its pollinators. As Fig. 2 shows, the
281 increase in the fruit and seed set of *R. sativus* was most pronounced between single- and
282 three-functional group communities. The increase in fruit and seed set from single to three-
283 species assemblages consisting of a single functional group was clearly less pronounced. The
284 nine-species communities, however, did not perform significantly better than the communities
285 consisting of three species from three functional groups, or their performance was even
286 slightly lower in the case of seed set. This suggests a saturating or, alternatively, a hump-
287 shaped relationship between species richness and pollination service [40–41]. However, our
288 analysis indicates that the latter did not adequately describe the observed patterns. A
289 saturating relationship between biodiversity and ecosystem functioning is predicted by niche
290 theory assuming complementary resource use but increasing niche overlap with increasing
291 richness, and systems characterised by rather generalised interactions [29, 42–44]. A hump-
292 shaped relationship between pollinator richness and pollination service is predicted, if
293 increasing species richness leads to a lower proportion of visits a plant receives by the more
294 effective pollinator species [30, 40].

295 In a previous study using caged pollinator communities, Fontaine *et al.* [19] could
296 show that pollinator communities containing the two functional groups hoverflies and social
297 bees can increase aggregated plant reproductive success of plant communities consisting of
298 species with open vs. tubular flowers, compared to single functional-group assemblages, due
299 to morphological constraints in short-tongued hoverflies to pollinate plants with tubular
300 flowers, while more efficiently pollinating open flowers. In this case, similar to experiments

301 with plant or bacterial communities, the functional consequences of diversity were stronger in
302 more heterogeneous resource environments [45–46]. In contrast, our study is among the first
303 to experimentally demonstrate positive effects of pollinator richness in a more homogeneous
304 pollinator resource environment, namely that of a single plant species. From the plant's point
305 of view this indicates that even at the population level a diverse pollinator community may
306 increase plant reproductive success.

307 Apart from the study of Fontaine *et al.* [19] and the present study, existing evidence
308 for positive effects of pollinator species diversity on pollination services comes mainly from
309 correlational studies of animal-pollinated crop (e.g. [10, 12, 16]) and wild plant species [13,
310 40]. Some of these correlations between pollinator diversity and pollination service have been
311 attributed to temporal complementarity among years [10] or combined spatio-temporal
312 complementarity [16]. However, collinearity among aggregate abundance and diversity of
313 pollinators in these studies makes it difficult to assess the importance of different components
314 of pollinator diversity and the mechanisms driving the observed patterns [20, 21]. Indeed, a
315 recent simulation study suggested that similar functional patterns may arise from the
316 relationship between relative abundance and the effectiveness of the pollinator species present
317 in diverse communities [30]. Our results demonstrate positive pollinator diversity effects on
318 pollination services and plant reproductive success that are independent of aggregate
319 pollinator abundance.

320 Despite the clear need for controlled experiments to address some of the important
321 aspects of the functional consequences of pollinator diversity [19–21], they come at the cost
322 of simplifying some of the real-world complexity. Cages represent an artificial environment to
323 pollinators, hindering them in the performance of some types of natural behaviours, such as
324 the provisioning of nests in the case of bees. However, in agreement with observations of
325 Fontaine *et al.* [19], visitation rates and duration of flower visits of foraging pollinators were
326 in the range of those observed under natural conditions for the model plant species (M.

327 Albrecht, unpublished data). Pollinator communities of a generalised plant species such as *R.*
328 *sativus* are likely to be more species rich, at least those of plant populations in relatively un-
329 degraded habitats [13, 40]. From our study using a relatively low maximum pollinator
330 number, we cannot rule out the possibility that at considerably higher levels of pollinator
331 richness the richness–pollination service relationship becomes humped-shaped [40] if
332 negative selection effects due to many highly inefficient pollinators or nectar-robbing flower
333 visitors [47] play a more important role. Furthermore, it is conceivable that at high richness
334 antagonistic pollinator interactions in the simple one-resource plant environment, e.g. through
335 disturbance or even competitive exclusion of functionally superior pollination service
336 providers by inferior ones from some pollination niches, could lead to negative
337 complementarity effects. Such increases in antagonistic interactions in simple resource
338 environments leading to negative biodiversity effects have recently been found in bacterial
339 biodiversity–ecosystem functioning experiments [45, 48]. More complex resource
340 environments including larger temporal and spatial scales are expected to considerably
341 broaden the scope for complementarity effects and associated increased ecosystem
342 functioning [18, 49–51].

343

344 *What are the drivers of the positive pollinator richness effects?*

345 Our results indicate that the presence of social bees in a community was an important factor
346 explaining positive pollinator richness effects on seed set, and in particular fruit set, of *R.*
347 *sativus*, suggesting that a positive selection effect [25] played an important role in the
348 observed diversity effects. Indeed, social bees visited roughly four times more flowers than
349 solitary bees or hoverflies, and the three social bee species showed the highest pollination
350 service, measured as fruit and seed set, in the single-species treatments. The pollinator species
351 providing the highest pollination service was the bumblebee *B. pascuorum*.

352 However, we found strong evidence that — in addition the higher overall visitation
353 rates of social bees — niche complementarity was a key mechanism driving the positive
354 pollinator richness–pollination service relationship: the three functional groups differed in
355 their relative foraging activity at different times of the day — social bees showing particularly
356 distinct diurnal visitation patterns compared to solitary bees and hoverflies —, and they
357 tended to differ in the relative number of flowers visited at different heights within plants.

358 By exploiting different spatio-temporal niches, pollinators can maximize their
359 resource-use efficiency, while simultaneously increasing pollination efficiency at the
360 community level [20, 21]. Diurnal foraging activity is determined by intrinsic factors, such as
361 physiological attributes and environmental tolerances, and behavioural responses in relation to
362 the daily course of extrinsic factors [52] that may result in pollinator species-specific or
363 pollinator group-specific “daily activity windows” [31, 49, 53, 54]. In our study solitary bees
364 foraged most in the morning, hoverflies in the morning and noon and social bees in the
365 afternoon. Similarly, peak visitation rates of bumblebees and honeybees in the afternoon have
366 been observed for other wild plant and crop species in temperate climates, which have mostly
367 been attributed to positive temperature–foraging activity relationships (e.g. [55]). Our findings
368 are also in agreement with the scarce existing data on diurnal foraging activity of hoverflies,
369 suggesting that pollen feeding of most species is highest in the morning hours [56]. Previous
370 observations of foraging activity patterns of solitary bees indicate that they can be highly
371 variable, with some solitary bee species visiting more flowers in the morning than in the
372 afternoon [57], while others show bimodal patterns with peaks in the morning and afternoon
373 [31]. In our study social bumblebees and honeybees, in contrast to the other pollinator groups,
374 also continued to forage after 18 h (M. Albrecht, personal observation). In many plant species,
375 including *R. sativus*, stigma receptivity is rather short (usually a few hours) and can show
376 some variation among plant individuals during the day [37], which could have contributed to
377 the importance of diurnal complementarity in pollinator foraging activity.

378 Spatio-temporal niche partitioning in pollinator communities is likely to be greatest in
379 heterogeneous or plant species-rich landscapes that offer a broad array of niches to be
380 partitioned [20, 51]. This is in accordance with the general finding that biodiversity effects
381 increase with biotope space [46]. Indeed, our results indicate that even within a simple
382 environment with a single flowering plant as a resource such spatio-temporal niche
383 partitioning was effective, with the temporal component of complementarity in diurnal
384 visitation times being clearly more important than the spatial component of complementarity
385 in flower visitation heights.

386

387 *Conclusions*

388 Our study demonstrates enhanced pollination-mediated reproductive success in a single plant
389 species due to higher pollinator functional-group richness — and if only one functional group
390 is present also at higher species richness — independent of aggregate pollinator abundance.
391 Such fine-scale functional effects of pollinator richness are likely to be important for the
392 population dynamics of local populations of natural plant species, and have economic
393 implications for the many animal-pollinated plant crops worldwide, which are typically grown
394 as monocultures of single plant species [6]. In agreement with predictions of biodiversity–
395 ecosystem functioning relationships for simple resource environments, highest species
396 richness resulted in slightly reduced pollination services compared to intermediate levels of
397 species richness. Our results suggest that both, complementarity effects, primarily resulting
398 from different realized daytime niches among pollinator functional groups, and the presence
399 of particular taxa in a pollinator community, in our case social bees, contributed to the
400 positive pollinator richness–pollination service relationship. These findings provide an
401 important step towards a more mechanistic understanding of the effect of pollinator diversity
402 on pollination services. Our results emphasize the importance of the conservation and

403 restoration of diverse pollinator communities for the provisioning of pollination services to
404 animal-pollinated plants.

405

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413

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575

576 **Figure legends**

577 **Fig. 1** Experimental design. Increasing pollinator richness up to nine species and three
578 functional groups (social bees (A), solitary bees (B) and hoverflies (C)), including all single-
579 species “communities”, were used in a substitutive design. Three-species communities
580 contained one or three functional groups. Communities with three species from three
581 functional groups did not overlap.

582

583 **Fig. 2** (a) Mean (± 1 standard error) number of seeds per fruit and (b) mean number of fruits
584 per flower of *R. sativus* at different levels of pollinator functional group (social bees, solitary
585 bees, hoverflies) and species richness (see Fig. 1 for the experimental design).

586

587 **Fig. 3.** Mean (± 1 standard error) number of flower visits during 30 min of the three
588 functional groups social bees, solitary bees and hoverflies at four different daytime periods:
589 9.00–11.30 h, 11.30–14.00, 14.00–16.30, 16.30–19.00.





