

1 **The vulnerability of plant-pollinator communities to honeybee decline: a comparative**
2 **network analysis in different habitat types**

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20
21 **Abstract**

22 The populations of most pollinators, including honeybees, are declining that heavily affects
23 both crop and wild plant pollination. Wild bee diversity and habitat type may modulate these
24 effects. We addressed the question how the structure of plant-pollinator networks in different
25 habitat types may influence the vulnerability of pollinator communities to the hypothetical
26 loss of honeybees. We performed network analysis based on plant-visitation data in a
27 traditional agricultural landscape and quantified the structural vulnerability (i.e. the effect of
28 the loss of honeybee) of the plant-pollinator networks by a topological index (distance-based
29 fragmentation). We found that very different plant-pollinator communities inhabited the
30 studied different agricultural habitat types. The early summer arable fields had the most,
31 pastures in mid-summer had the less vulnerable structure and, in general, an intermediate
32 plant/pollinator ratio is was associated with high vulnerability in the absence of honeybees.
33 We suggest that increased plant species richness can ensure higher wild bee diversity and
34 more stable plant-pollinator networks without honeybee, where flower-visitation can rely

35 more on wild bees. Decreased management intensity in agricultural landscapes can therefore
36 contribute to the maintenance of diverse plant-pollinator communities in agricultural
37 landscapes and to sustainable farming.

38

39 **1. Introduction**

40

41 Ecosystem services like pollination (Daily, 1997; Ollerton, 2017) may be better managed if
42 the evolutionary ecology of the underlying processes is better understood (Bronstein, 2001).
43 In the age of the pollination crisis (Ghazoul, 2005; Potts et al., 2016; IPBES, 2016), it is a
44 major challenge to better understand the ecological and economical aspects of pollination as
45 an ecosystem service. The decline of pollinators seems to be strongly related to agricultural
46 activities at both local and landscape scales (Carvell et al., 2017; Kovács-Hostyánszki et al.,
47 2017). Such disturbance, however, might have no visible effect on the number of foraging bee
48 species, while disturbance can reduce the number or frequency of bee and flower interactions,
49 and consequently foraging and pollination success (Carman and Jenkins, 2016). This calls for
50 an explicit analysis of plant-pollinator communities along a gradient of human influence.

51 Western honeybee (*Apis mellifera*) is widely used, managed pollinator, responsible for
52 pollination of highly commercial crops (e.g. almond, cherry, apple, etc.; Abrol et al., 2012),
53 but it is also important supergeneralist pollinator in wild plant communities (Giannini et al.,
54 2015; Hung et al., 2018; Kovács-Hostyánszki et al., in prep). The exclusive dependence on
55 honeybees, however, has several risks. On the one hand honeybees show massive decline in
56 several parts of the world (Goulson et al., 2015; IPBES 2016) that can be balanced by
57 beekeepers in a certain extent dividing existing colonies, but still the number of honeybee
58 colonies cannot keep up with the even faster growing of insect-pollination demand of
59 agricultural crops (Aizen et al., 2009). On the other hand, honeybees are capable for effective
60 pollination only among favourable weather conditions (Brittain et al., 2013), and only for
61 certain plant species at limited extent (Garibaldi et al., 2013), while their pollination service is
62 often well supplemented, substituted by wild pollinators or even exclusively provided by them
63 (Aslan et al., 2016). Furthermore, the presence of honeybees within agricultural and (semi-)
64 natural habitats is strongly influenced by beekeeper activities (e.g. location and number of
65 colonies), and in natural habitats in 33% of plant-pollinator networks honeybee visit was not
66 even observed (Hung et al. 2018), which consequently rely on only wild pollinator species. To
67 conclude, the decline or lack of honeybees in agricultural and (semi-) natural habitats can be a
68 realistic scenario among different circumstances that can have a considerable but still partly

69 unknown effect on plant-pollinator communities. Looking at from the wild pollinators point
70 of view, wild bees and others face also the detrimental effects of land-use change, land
71 management and other effects such as pathogens, climate change, invasion (Goulson et al.
72 2015; IPBES 2016), therefore the stability of managed and semi-natural ecosystems against
73 wild bee decline is also questionable.

74 A systems approach to understand land use and land management effects and the
75 reliance of plant-pollinator communities on honeybee and wild bees is the analysis of plant-
76 pollinator networks that have been extensively studied in the last decades (Jordano, 1987;
77 Memmott, 1999; Olesen et al., 2002; Bascompte et al., 2003; Vamosi et al., 2006; Waser and
78 Ollerton, 2006; Bascompte, 2009; Kaiser-Bunbury et al., 2017; Guimarães et al., 2017; Soares
79 et al., 2017). The analysis of these mutualistic bipartite networks may help in quantifying
80 either their local (e.g. hubs, Biella et al., 2017) or global (e.g. nestedness, Podani et al., 2014)
81 properties, characterizing particular species or the whole community, respectively. Since
82 plant-pollinator interaction networks encompass the characteristics of species, their
83 interactions, and the evolutionary processes (Bascompte, 2007), they may be better indicators
84 of environmental change effects than species diversity (Tylianakis et al. 2010; Carman and
85 Jenkins, 2016; Soares et al., 2017).

86 In this paper, (1) we describe a large-scale, total plant-pollinator network for a
87 traditional agricultural landscape in Transylvania, Romania, (2) we analyse and compare its
88 16 subnetworks representing different habitat types (according to land use and land
89 management) and (3) we study the vulnerability of these networks to honeybee loss, using a
90 network measure imported from social sciences to ecology. We hypothesised that the
91 structure of plant-pollinator networks is different in different habitat types based on their land-
92 use, sown crop type or management in the case of grasslands, which may also influence the
93 vulnerability of their flower-visitation networks to the hypothetical loss of honeybees. We
94 expected higher vulnerability of those networks that are comprised by fewer plant and/or
95 pollinator species, whereas flower-visitation networks of floristically diverse habitats were
96 hypothesised to be more stable and based more on wild bees as flower visitors. Such
97 differences can be also expected within land-use or crop types depending on the season and
98 the availability of flowering plant species between months.

99

100 **2. Data: network construction**

101 We collected flower-visitation data in Southern Transylvania, Romania in 2012 (see map in
102 Kovács-Hostyánszki et al. 2016, S1. Fig), in 19 village catchments characterised by a

103 traditionally managed agricultural landscape of small parcels of low-intensity arable fields
104 (15%), pastures (40%) and deciduous forests (33%). In each catchment typically two arable
105 fields and two grasslands (land-use types) were chosen, which varied along different crop
106 and/or management types, including alfalfa (N=15), cereal (winter wheat and barley; N=8),
107 corn (N=8), fallow (N=4), grassland with shrubs (N=7), pasture (grazed by cattle or sheep;
108 N=24), hay meadow (N=10) and mowed grasslands or harvested arable fields (hereafter
109 stubbles; N=14). (for further details see Kovács-Hostyánszki et al., 2016). Landscape
110 composition around the study sites was considered by the calculation of percentage area of
111 semi-natural habitats (vineyards; fruit trees and berry plantations; pastures; complex
112 cultivation patterns; land principally occupied by agriculture, with significant areas of natural
113 vegetation; natural grasslands; transitional woodland-shrub) and Shannon index of land cover
114 diversity (land cover categories: urban, arable, semi-natural, forest, water) within 1000 m
115 radius circle using CORINE land cover data (European Environment Agency 2013) and
116 ARCGIS software (ESRI 2008). We compared the two land-use types (arable vs. grassland)
117 and the eight crop and/or management types in the function of semi-natural area ratio and
118 Shannon habitat diversity in the 1000 m radius circle around the focal fields. We found that
119 arable fields and grasslands (t-test; $t = 0.37$, $df = 146.901$, $p\text{-value} = 0.711$) and the seven crop
120 and /or habitat types (Anova; $df = 6$, $F = 1.99$, $p = 0.070$) did not differ in the sense of habitat
121 diversity. The percentage of semi-natural habitats was higher around grasslands (that is a
122 semi-natural habitat itself; $t = -5.79$, $df = 147.252$, $p < 0.001$). Here especially pastures were
123 surrounded by higher percentage of semi-natural habitats compared to the arable fields
124 (Anova; $df = 6$, $F = 4.24$, $p < 0.001$; Tukey-test: pasture – cereal: 0.007; Appendix A).

125 We sampled flower-visiting bees by transect walk method along two parallel 100 m
126 long transects (1.5 m width either side) per field, at least 30 m from the edge and 50 m from
127 each other, over 20 min per transect once per month in May, June, July in 10-12 days periods
128 on dry and warm days with minimal wind, and 20°C minimum temperature, between 9 AM
129 and 6 PM. All bee specimens and plant species that were visited by the bees were identified at
130 species level.

131 Based on plant-visitation field data from 38 arable field and 38 grassland
132 communities, we created a „total” interaction network of 256 species: 123 plant (Appendix
133 **AB**) and 133 wild bee species (Appendix **BC**). For clarity, we omitted samples that were
134 impossible to taxonomically specify (e.g. individuals identified only at genus level) – these
135 represented only 3.65 % of individuals in the samples. The interaction network is a weighted

136 (by frequency of visits), undirected (effects spreading in both bottom-up and top-down
137 direction) and unsigned (all interactions are mutually positive) graph.

138 We note here that this pooled „total” network represents the plant-pollinator
139 community at a larger-scale, with lower spatial resolution (at the landscape level). We have
140 also studied 16 subnetworks of this „total” network, describing particular locations (habitat
141 types). We note that these communities (and the networks) are not perfectly independent of
142 each other (e.g. pastures are subsets of grasslands), they must be considered as various
143 appropriately defined subsets. Based on land use, we constructed separate networks for
144 grasslands (G) and arable fields (A). According to habitat type and land management, we
145 constructed separate networks such as shrubby grassland (SHG), cereal field (CEF), hay
146 meadow (HAM), cornfield (COF), pasture (PAS), stubble (STU), alfalfa (ALF) and fallow
147 (FAL). Moreover, based on existing temporal data series, for the grassland (G) and the arable
148 field (A) networks, we could construct interaction networks for May (G5 and A5), June (G6
149 and A6) and July (G7 and A7), where numbers refer to months. The details of these
150 communities and land use effects are studied and discussed in Kovács-Hostyánszki et al.
151 (2016).

152 Most of the networks contained either isolated species or smaller (dwarf) components
153 including only a few species. We focused on the giant component of the networks, presenting
154 also the pollinator species composition in the dwarf components (Appendix [€D](#)). We note
155 that the identity of components is perfectly consistent (a component with only species i and j
156 and another component with only species j and k imply the existence of a third component
157 with only species i and k). In the case of the total network, there was only a single dwarf
158 component (of two species), and this component was deleted together with all the isolated
159 nodes (species sampled in the field with no detected interaction partner).

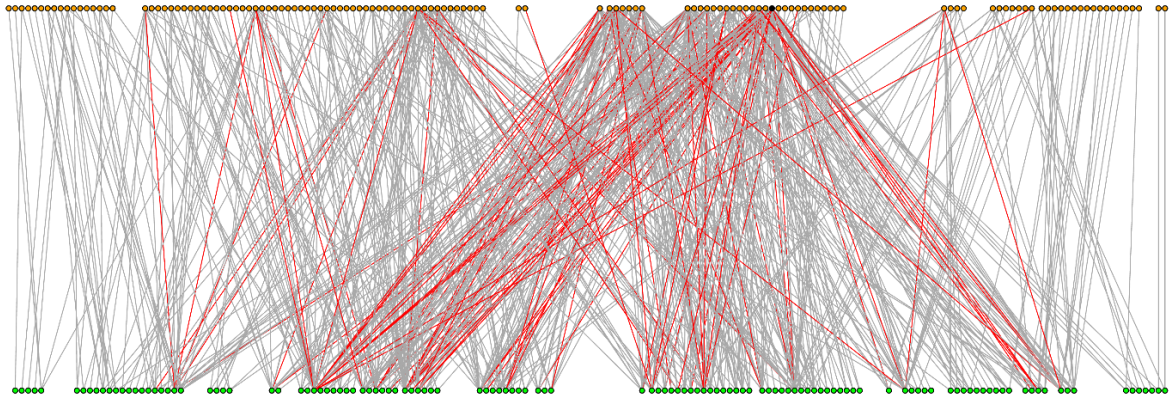
160 For the total network, we have also calculated the relative abundance values (RA_i) of
161 pollinators: this equals the number of individuals of species i per all identified individuals.
162 The sum of RA_i values equals one. We plotted the RA_i values with and without the honeybee
163 (APIMEL) in Appendix [ĐE](#): almost 35% of the pollinator individuals belonged to honeybee
164 (a), so the plot without honeybee (b) could show the abundance rank of further, wild bee
165 species.

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172 **Figure 1.** Topology of the aggregated total network. Orange and green nodes correspond to
173 wild bee pollinators and plants, respectively. Honeybee is marked by black and indicated by
174 an arrow. Interactions with a frequency value greater than 4 are red. We show only the giant
175 component of the network (by removing isolated nodes and dwarf components). Drawn by
176 igraph (Csardi and Nepusz 2006).

177

178 **3. Methods: network analysis**

179

180 Several methods have been used for studying mutualistic, bipartite networks in ecology
181 (Benedek et al., 2007; Blüthgen et al., 2006; Podani et al., 2014). In this paper, we studied
182 some global properties of the plant-pollinator networks, quantifying them by simple
183 topological measures. These network-level (macroscopic) indicators may quantify system-
184 level changes and ecosystem health, similarly to other types of ecological interaction
185 networks (Ulanowicz, 1996). Network-level topological metrics are increasingly used as
186 system-level indicators in different areas of ecology (Baranyi et al., 2011; Ortiz et al., 2017;
187 Pereira and Jordán, 2017).

188 In the case of each network, we were interested in the total number of nodes (N), as the
189 sum of the number of plant species (N_P) and the number of pollinator species (N_A):

190

191

$$N = N_P + N_A$$

192

193 These provide information about species diversity in the particular communities.

194

195 In several networks, there are isolated nodes (pollinators and plants where the species
196 are detected but no pollination interaction was detected for them), isolated pairs of nodes (a
plant and a pollinator in a mutually exclusive interaction) and also smaller sets of species (a

197 dwarf component) isolated from the majority of species in the community (giant component).
 198 Since the spread of direct and indirect effects needs connectedness in the network, we were
 199 interested in network components and quantified the number of nodes in the giant component
 200 (N_G), the number of dwarf components (d), the number of species in dwarf component(s) (N_d)
 201 and the percentage of nodes in the giant component ($G\%$).

202 In order to better understand interaction diversity, we calculated the ratio of plant and
 203 animal species (N_P/N_A), the number of plant-pollinator interactions (L) and the connectivity of
 204 the bipartite network (C):

205

$$206 \quad C = \frac{L}{N_P * N_A}$$

207

208 following the previous abbreviations. The distance between two nodes i and j in a network
 209 (d_{ij}) is the minimal number of links connecting them (i.e. the length of the shortest path
 210 between i and j). From this, their reciprocal distance is

211

$$212 \quad d_{ij}^r = \frac{1}{d_{ij}}$$

213

214 and this measure can be used when a network consists of more than one components (i.e.
 215 disconnected). Since the distance between nodes i and j equals infinity if they belong to
 216 different components, d_{ij} is not easy to use for disconnected networks. In this case, d_{ij}^r helps,
 217 since the reciprocal of infinity equal, by definition, zero. The distance-weighted fragmentation
 218 (F^d) of the network can be calculated as

219

$$220 \quad 1 - COM$$

221

222 where COM (compactness) is

223

$$224 \quad COM = \sum_{i,j}^N \frac{2 * d_{ij}^r}{i * j}$$

225

226 which is the average reciprocal distance for each pair of nodes in the network. The distance-
 227 weighted fragmentation of a particular node k is the difference of F^d between the networks

228 with and without node k . We studied here only the distance-weighted fragmentation for the
 229 honeybee (F^d_{APIMEL}). Several other, frequently studied topological metrics could have also
 230 been calculated but, for example, nestedness and modularity did not show major differences
 231 between vegetation types (Kishi et al. 2017) and different landscapes (Nielsen and Totland
 232 2013).

233

234 4. Results

235

236 The topology of the total network is shown in Figure 1. In this total network, honeybee
 237 (APIMEL) dominated the network also by abundance, its RA was almost 0.35 (i.e. each third
 238 individual was honeybee, Appendix [DE](#)). After the removal of the honeybee, RA values were
 239 more evenly distributed but still showed a quite skewed rank with 4-6 numerically dominant
 240 wild bee species (e.g. *Bombus terrestris*, *Halictus gavaranicus*, *Lasioglossum malachurum*, *L.*
 241 *pauillum*, *Andrena flavipes*). However, the in silico removal of honeybee is an easy way to
 242 simulate extinctions (see Memmott et al. 2004), switching mechanisms can certainly re-wire
 243 the network (but switching parameters are not really available). This network described the
 244 plant-pollinator community of the studied landscape in general, but our main question was
 245 how diverse was this network for different habitat types representing various land use
 246 scenarios.

247

web	SHG	CEF	HAM	COF	PAS	STU	ALF	FAL	G	G5	G6	G7	A	A5	A6	A7
N	98	52	71	26	159	8	83	72	198	63	108	122	159	47	91	95
N _G	78	46	65	24	152	4	79	69	198	55	105	122	153	25	81	91
d	8	3	3	1	3	2	1	1	0	3	1	0	2	4	4	2
N _d	20	6	6	2	7	4	4	3	0	8	3	0	6	22	10	4
G%	79,59	88,46	91,55	92,31	95,60	50,00	95,18	95,83	100,00	87,30	97,22	100,00	96,23	53,19	89,01	95,79
F ^d	0,78	0,70	0,72	0,64	0,70	0,77	0,68	0,69	0,68	0,74	0,66	0,69	0,69	0,86	0,74	0,67
F ^d _{APIMEL}	0,83	0,77	0,78	0,70	0,74	-	0,72	0,71	0,71	0,78	0,68	0,74	0,71	0,92	0,75	0,69
N _P	50	22	31	9	71	4	26	33	93	26	56	51	69	21	37	41
N _A	48	30	40	17	88	4	57	39	105	37	52	71	90	26	54	54
N _P /N _A	1,04	0,73	0,78	0,53	0,81	1,00	0,46	0,85	0,89	0,70	1,08	0,72	0,77	0,81	0,69	0,76
L	133	70	95	30	294	5	117	108	428	82	217	181	324	44	135	181
C	0,06	0,11	0,08	0,20	0,05	0,31	0,08	0,08	0,04	0,09	0,07	0,05	0,05	0,08	0,07	0,08

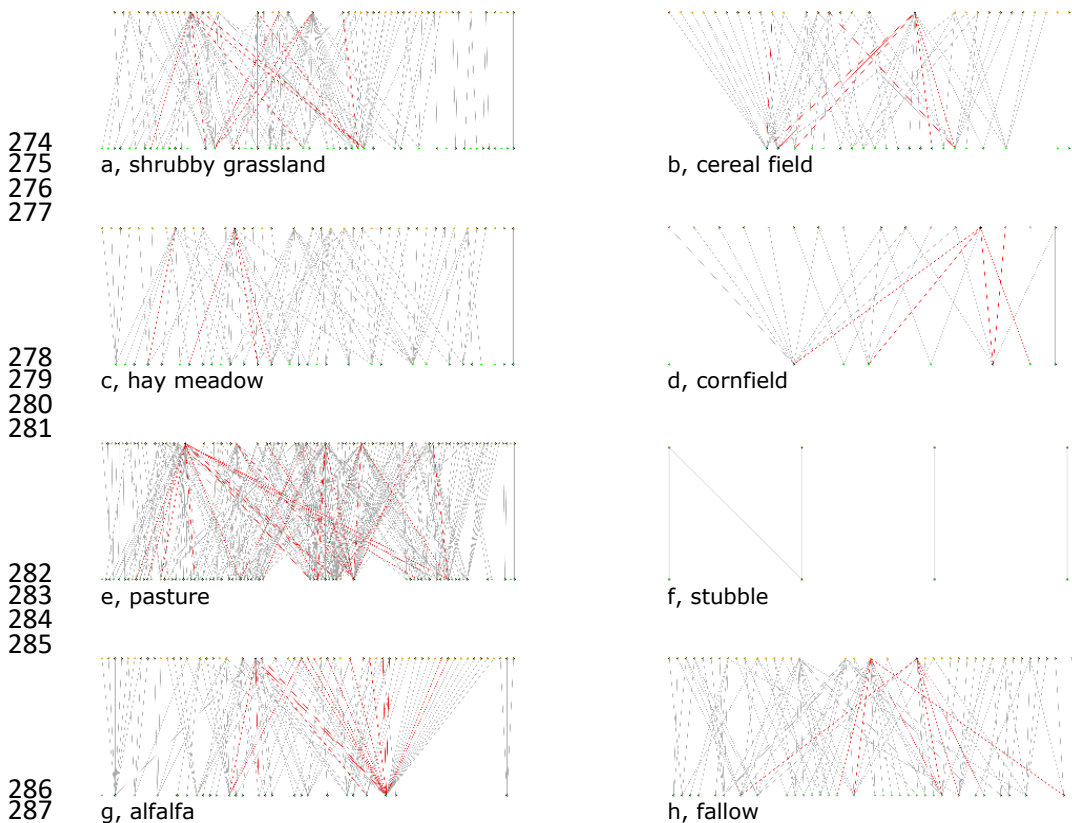
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250 **Table 1.** Network properties (N: number of nodes, N_G: number of nodes in the giant
 251 component, d: number of dwarf components, N_d: number of nodes in the dwarf component(s),
 252 G%: percentage of nodes in the giant component, F^d: distance-based fragmentation for the
 253 network, F^d_{APIMEL}: distance-based fragmentation for honeybee, N_P: number of plant species,
 254 N_A: number of pollinator species, N_P/N_A: the ratio of plants and pollinators, L: number of

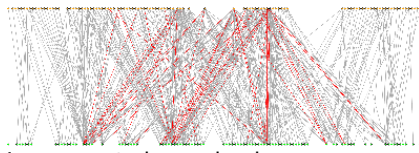
255 plant-pollination interactions, C: connectivity of the bipartite network) of the 16 particular
 256 networks (SHG: shrubby grassland; CEF: cereal field; HAM: hay meadow; COF: cornfield;
 257 PAS: pasture; STU: stubble; ALF: alfalfa; FAL: fallow; G: aggregated grassland; G5:
 258 grassland in May; G6: grassland in June; G7: grassland in July; A: aggregated arable field;
 259 A5: arable field in May; A6: arable field in June; A7: arable field in July). For the
 260 abbreviation of network properties, see the text. We provide the size distribution of dwarf
 261 components, however, it is not considered in the network analysis of the giant component.
 262

263 Figure 2 shows the topologies of the particular networks and Table 1 presents their
 264 quantitative properties. The size of arable network was kind of similar to the grassland
 265 network ($N_A = 159$ and $N_G = 198$, respectively) and in both networks most of the species
 266 belonged to the giant component ($G\% = 96.23\%$ and $G\% = 100\%$, respectively). The size of
 267 the different subnetworks varied widely: the network of the stubble community was quite
 268 simple with only $N_G = 4$ species (2 plants and 2 pollinators) in the “giant” component (and 4
 269 other species in two other components of size 2, see Appendix [ED](#)). Another small but
 270 slightly more speciose community was found in the cornfields. The shrubby grassland, cereal
 271 field, hay meadow, alfalfa and fallow communities were of medium size, while the pasture
 272 communities were really speciose.
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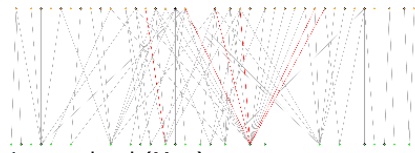


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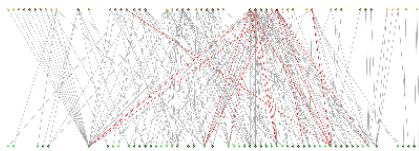


i, aggregated grassland

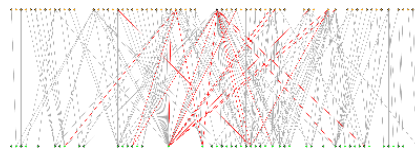


j, grassland (May)

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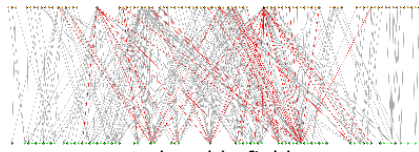


k, grassland (June)

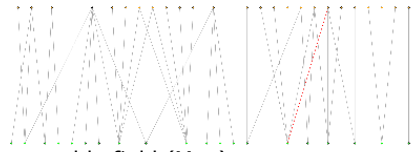


l, grassland (July)

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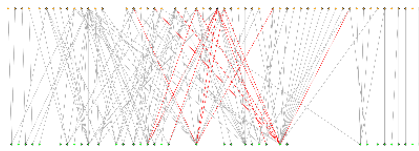


m, aggregated arable field

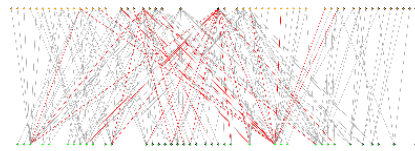


n, arable field (May)

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o, arable field (June)



p, arable field (July)

304

305 **Figure 2.** Topology of the different particular subnetworks of Figure 1. Interactions with a
306 frequency value greater than 4 are red. Only the giant components are shown (by removing
307 isolated nodes and dwarf components), except for the STU network that is so small that
308 defining a “giant” component does not really make sense (so we show the whole network).
309 The names of particular communities are indicated. Drawn by igraph (Csardi and Nepusz
310 2006).

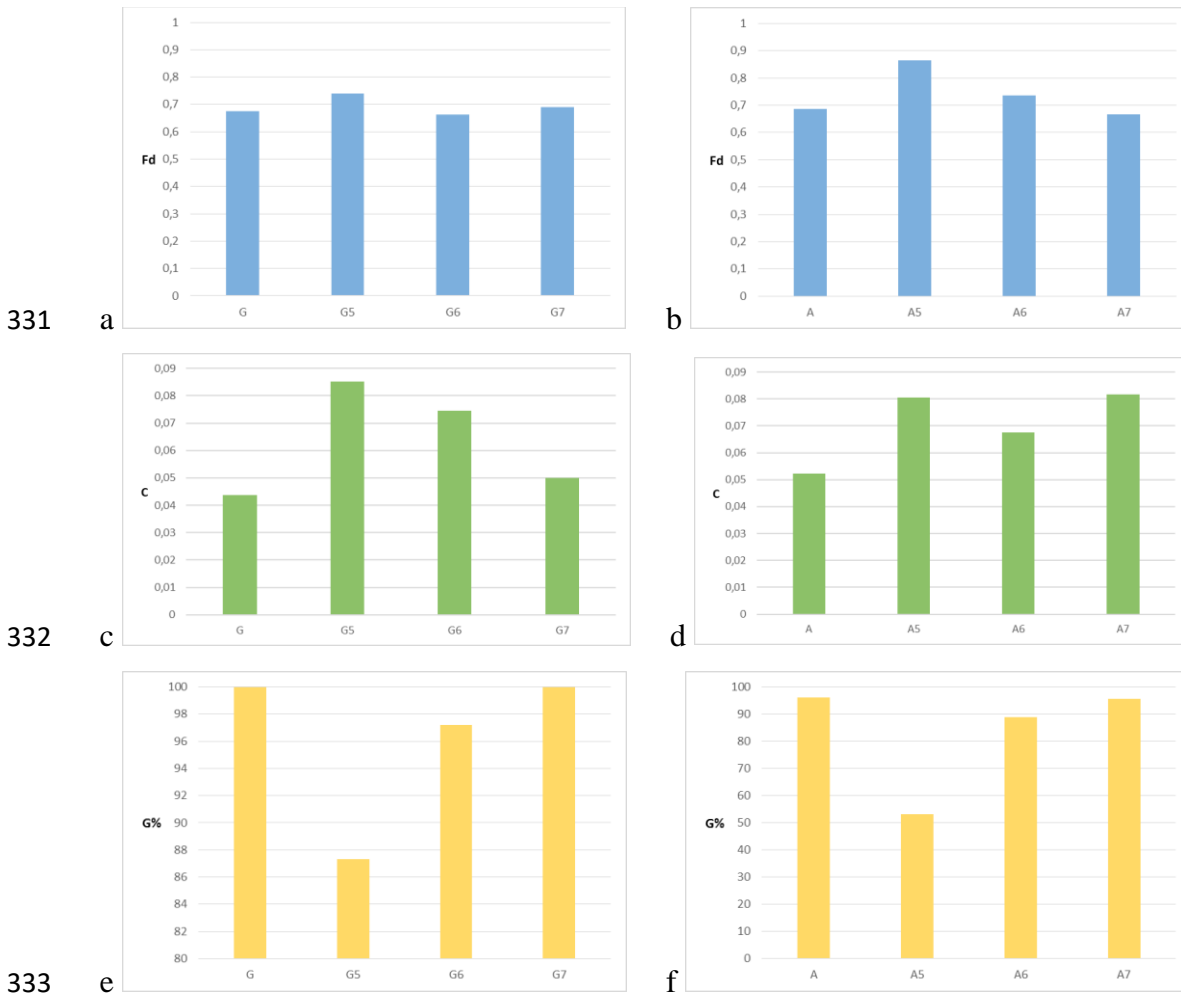
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312 Table 1 shows the size of the giant component and the dwarf component(s) for each
313 network. In most cases, a giant component dominated the network, containing an average of
314 87.95% of all species (the minimum was 50% and the maximum was 100%). Some
315 pollinators appeared only in a dwarf component in a particular interaction network. For
316 example, *Halictus confusus* (HALCON) pollinated only *Solanum tuberosum* in the cornfield
317 (COF) community (see dwarf components in each networks in Appendix [ED](#)). In general,
318 either plant or pollinator species in dwarf components (or in total isolation) can be more
319 vulnerable to environmental changes, since the replacement of their partner is more difficult.
320 In different habitats, very different species composed the dwarf components, so this kind of
321 interactions-based vulnerability is quite site-specific. But variability does not mean

322 randomness: species composition in dwarf components is perfectly nested: it never happens
 323 that species [A B], [A C] and [B C] form dwarf components in 3 particular habitats.

324 The number of plant (N_P) and pollinator (N_A) species, as well as their ratio (N_P/N_A)
 325 were also quite variable. The grassland in June (had the highest plant diversity compared to
 326 animal diversity $N_P/N_A = 1.08$), while the alfalfa community had the lowest ($N_P/N_A = 0.46$).
 327 The average N_P/N_A ratio was 0.79 for all the 16 networks.

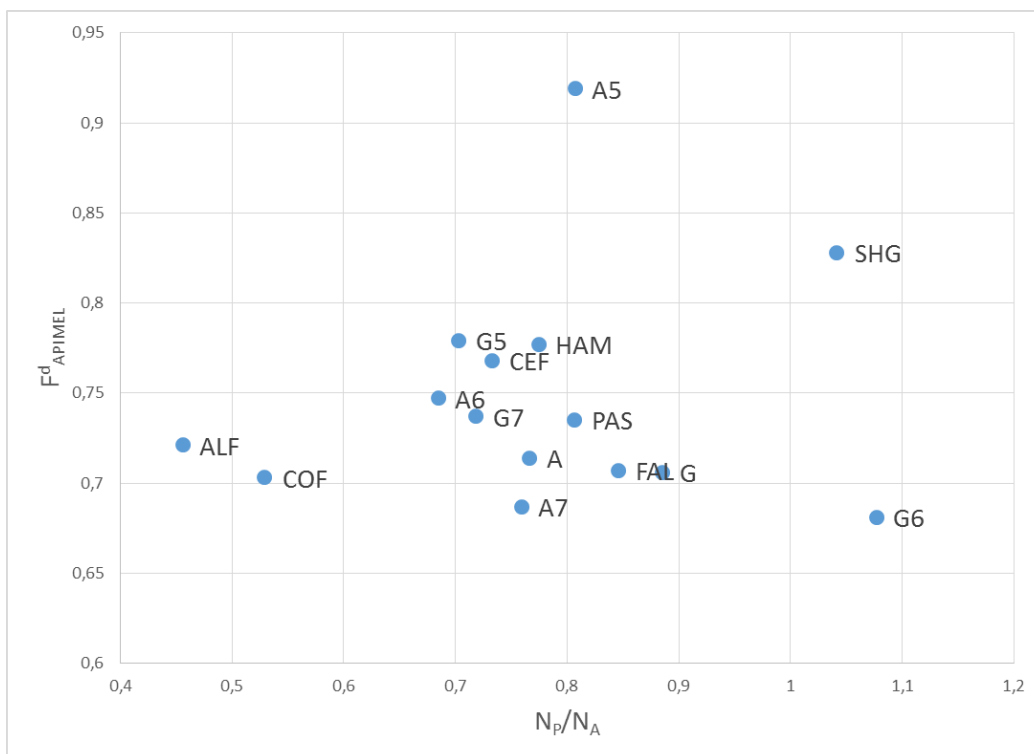
328 Considering also the number of interactions, the connectivity of these bipartite graphs
 329 (C) can also be given. It ranged from a minimum for grasslands ($C = 0.04$) to a maximum for
 330 stubble ($C = 0.31$), with an average of $C = 0.09$.



334
 335 **Figure 3.** Various properties of the aggregated networks (G = grassland, A = arable field) and
 336 their monthly series from May to July (e.g. A5 = arable field in May, G7 = grassland in July):
 337 fragmentation (F^d ; a: grassland, b: arable field), connectivity (C ; c: grassland, d: arable field)
 338 and giant component ratio ($G\%$; e: grassland, f: arable field).

339

340 The grassland and the arable field communities were described also in time: the
 341 phenology of the three summer months was determined. The size of the network increased by
 342 time in both grassland (Fig. 2i-l.) and arable (Fig. 2m-p) communities (Table 1). In both
 343 communities, the proportion of species belonging to the giant component ($G\%$) increased,
 344 mostly from May to June (Fig. 3e, 3f). From May to July, distance-weighted fragmentation
 345 (F^d) showed a decreasing tendency in the arable field community (Fig. 3b). In the same
 346 period, connectivity (C) showed a decreasing tendency in the grassland community (Fig. 3c).
 347 The change of fragmentation in the grassland (Figure 3a) and the change of connectivity in
 348 the arable field (Figure 3d) were not monotonous. Based on distance-weighted fragmentation
 349 (F^d), the arable field in May was the most vulnerable community in general ($F^d = 0.86$), while
 350 the cornfield was the most stable ($F^d = 0.64$). The fragmentation value of the honeybee was
 351 quite similar, the arable field in May being the most vulnerable to honeybee loss ($F^d_{APIMEL} =$
 352 0.92), while the grassland in June was the most stable against honeybee loss ($F^d_{APIMEL} = 0.68$)
 353 (Fig. 4).
 354



355
 356
 357 **Figure 4.** The relationship between F^d_{APIMEL} and N_P/N_A . The studied communities are more
 358 sensitive to honeybee loss with an average plant/animal ratio: with a disproportionately low or
 359 high plant/animal ratio, the loss of honeybee does not cause a large fragmentation effect on
 360 ecological interactions.

361

362 **5. Discussion**

363

364 In multi-species ecological communities, direct and indirect inter-specific effects are crucial
365 for the coexistence and coevolution of species. Ecological interaction network models show
366 the possibilities and limitations on effects spreading through these interactions. In better
367 connected networks, there are several pathways supporting inter-specific effects and
368 coevolution, while in more fragmented networks species depend on and they are influenced
369 by fewer partners. Human disturbance can modify interaction networks and ultimately the
370 functioning of the whole multispecies system.

371 The structural variability of plant-pollinator networks influences the vulnerability of
372 pollinator communities against compositional changes (e.g. honeybee loss or decline) and
373 environmental disturbance (e.g. land use change or land management effects, Kovács-
374 Hostyánszki et al., 2017). Our quantitative, system approach to better understand mutualistic
375 communities revealed major differences among different plant-pollinator networks within the
376 same agricultural landscape that can help to support ecosystem management.

377 Based on most macroscopic network indicators, very different plant-pollinator
378 communities inhabited the different agricultural habitat types. These compositional and
379 structural network properties do have an effect on community dynamics and ecosystem
380 functioning. Bees are strongly connected with flower resources seeking for nectar and pollen,
381 therefore their presence mostly depends on these available foraging resources (Fründ et al.,
382 2010; Rollin et al., 2015). A habitat with low number of flowers results in low bee abundance,
383 while low flowering plant diversity is usually associated with low bee diversity (Ebeling et
384 al., 2008; Fründ et al., 2010). High species diversity and community complexity of wild bees
385 in grasslands was clearly related to higher nectar quantity compared to arable fields (Baude et
386 al., 2017). The quite similar sized arable and grassland networks suggested a rather extensive
387 management in both land-use types and high amount of available wild flower resources (i.e.
388 weeds) also in arable fields. Although weeds are treated as serious competitors of crops
389 hampering crop production, they play major functional roles for agricultural biodiversity and
390 ecosystem services, especially pollination (Bretagnolle and Gaba, 2015; Rollin et al., 2016).
391 This is an important feature of the studied traditional low-intensity agriculture landscapes,
392 where partly due to topographical and historical issues the smallholder farming practices were
393 still preserved and inhabited by high weed and in general agro-biodiversity (Kovács-
394 Hostyánszki et al., 2016).

395 Among our studied subnetworks stubble fields were lately harvested or mown fields
396 just before the samplings, consequently only few remaining flowers were found there, visited
397 by a little number of bees. The second smallest network was found in the cornfields that were
398 ploughed and sown in spring. This recent soil disturbance prevented diverse plant and
399 pollinator communities (Nicholls and Altieri, 2013), but nevertheless a richly connected
400 network was found, where most of the species were part of the giant component. The autumn-
401 sown cereal fields, the left over fallows, and from the grassland habitat types the shrubby
402 grasslands and hay meadows hosted medium-sized plant-pollinator communities with a kind
403 of equal ratio of bees and visited plant species, while alfalfa fields showed twice as many bee
404 as plant species. Alfalfa (*Medicago sativa*) provides locally very abundant mono-floral
405 resources for pollinators that can attract both honeybees and wild bees, however its deep
406 flowers are more accessible for long-tongued bumblebees and specific genera of solitary wild
407 bees (e.g. *Andrena*, *Halictus*, *Lasioglossum*, *Megachile*, *Melitta*, *Xylocopa*) (Rollin et al.,
408 2013). Besides alfalfa is a permanent crop that enhances the presence of several other wild
409 plant species within the field. Pasture communities were the most speciose both in plant and
410 wild bee species. These permanent grasslands are grazed mostly by sheep at low intensity and
411 are important refuges for flowering plant species all over the season (Loss et al., 2014;
412 Kovács-Hostyánszki et al., 2016). Furthermore grasslands and especially pastures were
413 surrounded in 1000 m radius scale by higher ratio of semi-natural habitats. Pastures are also
414 semi-natural fields having usually higher spatial expansion, and they are usually situated at
415 higher elevation and less accessible places that probably resulted in this higher semi-natural
416 habitat ratio in their 1000 m environment. Such a more natural environment could have also a
417 rather positive effect on wild bee diversity and abundance, and hence an effect on plant-
418 pollinator networks (Winfree et al. 2009, 2011, Kovács-Hostyánszki et al. 2017). In the
419 grassland network all species belonged to the giant component, and in most cases, a giant
420 component dominated the sub-networks too. The number of dwarf components or the number
421 of species within the dwarf components varied among the different sub-networks and we
422 found no clear relationship with any other network properties.

423 Looking at the temporal changes in grassland and arable field networks we found that
424 the size of the network and the proportion of species belonging to the giant component
425 increased by time in both arable and grassland communities, showing a bigger difference
426 between May and June and only a slightly increase from June to July. It is basically in line
427 with the increase of flowering plant species from May to June and the activity peak of most of
428 the wild bee species in early mid-summer (Michener, 2007; Rollin et al., 2015). Considering

429 also the number of interactions, connectivity (C) showed a decreasing tendency in the
430 grassland community over time, while distance-weighted fragmentation (F^d) showed a
431 decreasing tendency in the arable field community, suggesting increased compactness.

432 While honeybee has an outstanding role in many of the crops' pollination, it had the
433 highest relative abundance in our studied total plant-pollinator network, being each third
434 individual of flower visitors of the mostly wild plant species. Western honeybee is a widely
435 managed species also in Romania, where honey market is 100% self-supply, beekeeping
436 sector is characterized by a fast dynamic during 2000-2010 and supply of honeybees is
437 relatively high compared to the pollination demand of insect-pollinated crops (Pocol et al.,
438 2012; Breeze et al., 2014). Our result is in line with a recent study based on a global dataset of
439 80 published plant-pollinator interaction networks as well as pollinator effectiveness
440 measures from 34 plant species in natural habitats, which found that the western honeybee
441 was the most frequent floral visitor, averaging 13% of floral visits across all networks (range
442 0-85%; Hung et al. 2018). We found that the structural importance of honeybee was largest
443 with an average plant/animal ratio (N_P/N_A). The alfalfa community (with low plant/animal
444 ratio) and the grassland community in June (with high plant/animal ratio) were quite stable
445 against the loss of honeybee, while the communities with intermediate plant/animal ratios
446 (e.g. hay meadow, arable field in May) were the most structurally vulnerable ones. While
447 long-term changes characterize pollinator diversity (Baude et al., 2017), our findings about
448 the unimodal change of honeybee importance with the plant/animal ratio support the presently
449 outstanding importance of honeybee, especially in crop fields. Arable fields especially in
450 springtime are still relatively flower poor and often disturbed habitats, therefore they might
451 better rely on generalist species such as honeybee for crop and wild plant pollination (Carman
452 and Jenkins, 2016). There are certainly differences among crops based on their reliance on
453 honeybee pollination, and potential decline and disappearance of honeybee would have
454 certainly important economic consequences. Some relevant crop and fruit tree species in the
455 Central-European region, such as sunflower (*Helianthus annuus*), apple (*Malus sylvestris*),
456 cherry (*Prunus* subg. *Cerasus*) are suggested to be primary or most abundantly pollinated by
457 honeybees (Abrol et al., 2012), however as Garibaldi et al. (2014) pointed out, wild insect
458 visitation had stronger effects on fruit set than honey bee visitation in most of these crop
459 systems too. Other crops such as alfalfa for example is poorly pollinated by honeybees, since
460 its deep flowers are more accessible for wild bee species having longer tongue (e.g. *Bombus*
461 ssp., *Megachile* ssp.; Abrol et al., 2012). Species rich natural habitats (i.e. grasslands in June),
462 however, seem to be stable without honeybee, relying on flower-visitation by wild bees.

463 Moreover, according to Hung et al. (2018) for one third of plant-pollinator networks and half
464 of the plant species in natural habitats honeybee visitation was never observed, highlighting
465 the importance of wild pollinators for many flowering plant taxa.

466 One limitation of studying these bipartite networks is that data typically describe
467 visitation frequency, while the act of pollen transfer or getting reward would be more
468 functional, biologically more relevant observations (Alarcón, 2010). Another issue to consider
469 is that these mutualistic communities are subsets of larger ecological communities: both the
470 plants and the pollinators have a number of other partners (e.g. parasites, see Klein et al.,
471 2017), so neither the structure nor the dynamics of these sub-networks can tell the whole
472 story. Yet, focusing on a bipartite network (Bascompte et al., 2006; Soares et al., 2017) is a
473 quantitative tool providing comparative knowledge on several systems, including spatial and
474 temporal series (cf. temporal changes in pollinator diversity, Baude et al., 2016; bee-flower
475 interaction networks along a disturbance gradient, Carman and Jenkins, 2016).

476 Future extensions of this study may better focus on the importance of weights (by
477 comparing weighted and binary networks) and they may compare visitation networks to
478 networks where interactions are determined by pollen analysis (Alarcón et al., 2010;
479 Ballantyne et al., 2015). Further, aggregating species into larger functional groups would be a
480 probably interesting research direction (aggregation based on either traits or network
481 topology; Garibaldi et al., 2015), while some patterns at the network level can be better
482 understood in the light of metrics analysed at the species level (Soares et al., 2017; Kovács-
483 Hostyánszki et al., in prep). It should be also important to merge plant-pollinator interactions
484 with others in unified models (see Losapio et al., 2015). As of particular interest, both from a
485 network dynamics point of view and also biologically, we have to better understand dwarf
486 components: why are these species not connected to the giant component and how could they
487 be connected (through which other species)? If we can understand the evolutionary ecology of
488 being out of the giant component, we may get a better framework for the conservation and
489 management of the whole system.

490 In summary, we found that honeybee clearly dominates the total, aggregated plant-
491 pollination network of the whole area. Its network position widely differs in various
492 subnetworks that are of different size and fragmentedness. The loss of honeybee seems to
493 cause the largest structural changes in subnetworks with an average plant/animal ratio. In
494 order to assess the possible consequences of future declines and invasions, a large-scale
495 comparative analysis of geographically distant networks can be informative. Different species
496 are the dominant crop pollinators in different ecoregions (Kleijn et al., 2015), and their

497 neighbourhood could be predictive for their ecological function in new environments. In order
498 to better understand and protect these communities, it is crucial to focus conservation on their
499 interaction structure and further improve the methodology here (Biella et al., 2017).

500

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502

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509

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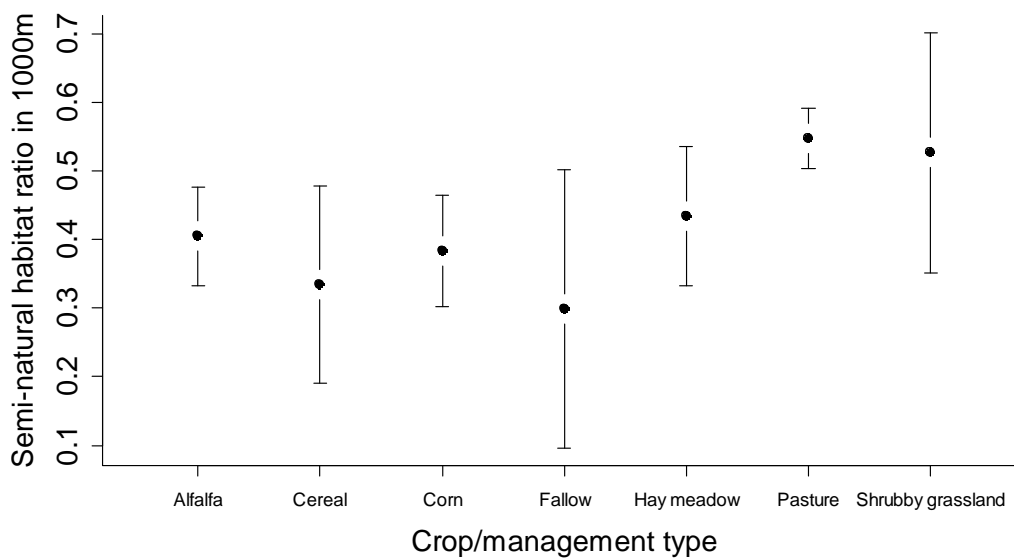
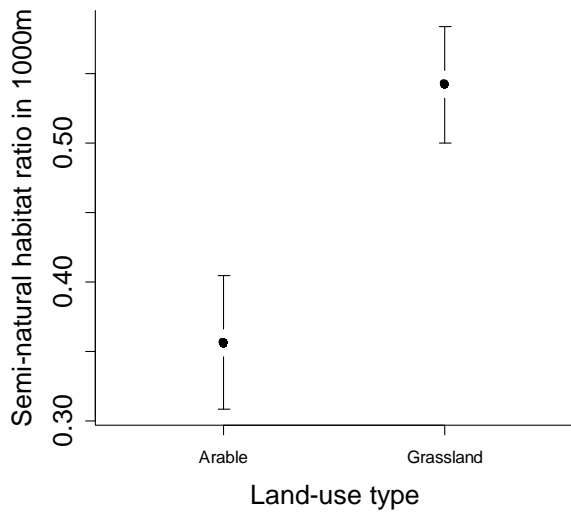
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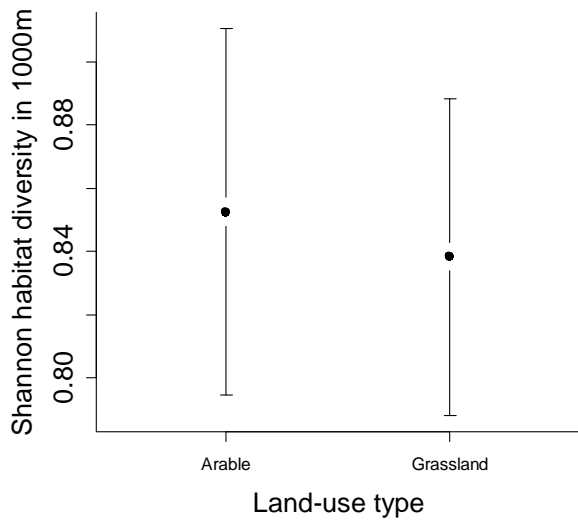
760 Appendix A. Ratio (mean \pm 95% CI) of semi-natural habitats (a) and Shannon habitat
761 diversity (mean \pm 95% CI) around the studied arable fields and pastures and the different crop
762 and/or habitat management types.

763 (a)

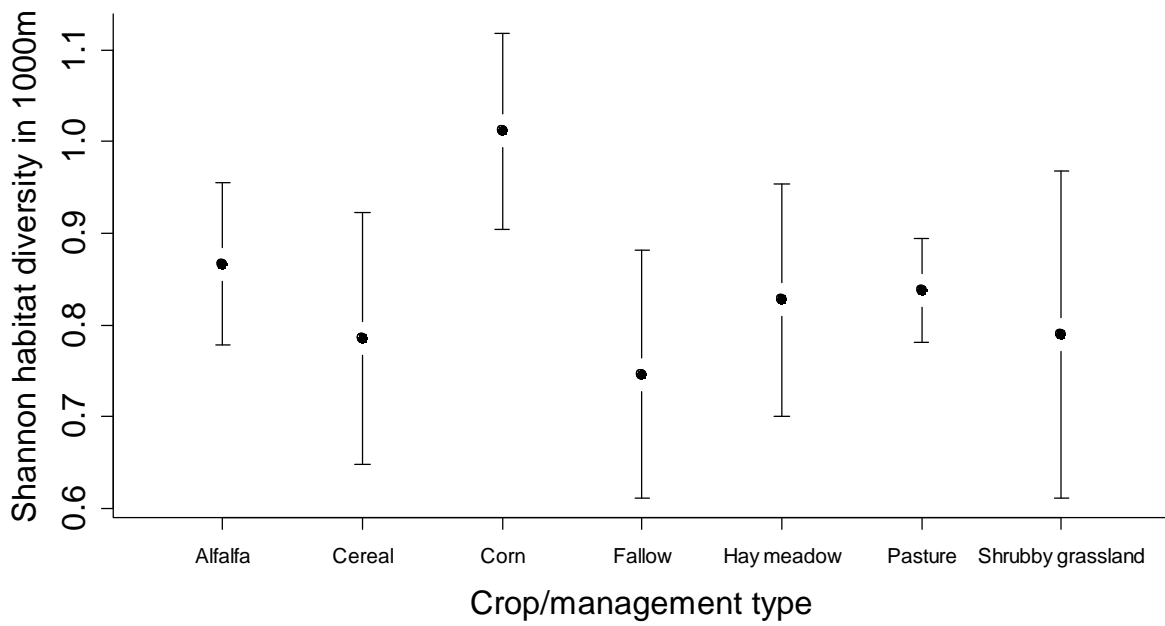


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(b)



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771 **Appendix AB.** The names of the 123 plant species appearing in the studied plant-pollinator
772 communities.

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<i>Achillea collina</i>	<i>Fragaria viridis</i>	<i>Nepeta cataria</i>	<i>Rorippa sylvestris</i>
<i>Adonis aestivalis</i>	<i>Galeopsis bifida</i>	<i>Nonea pulla</i>	<i>Salvia nutans</i>
<i>Agrimonia eupatoria</i>	<i>Galium mollugo</i>	<i>Onobrychis viciifolia</i>	<i>Salvia pratensis</i>
<i>Ajuga genevensis</i>	<i>Galium verum</i>	<i>Ononis arvensis</i>	<i>Salvia verticillata</i>
<i>Anthericum ramosum</i>	<i>Genista sagittalis</i>	<i>Origanum vulgare</i>	<i>Satureja hortensis</i>
<i>Asclepias syriaca</i>	<i>Gentiana cruciata</i>	<i>Ornithogalum brevistylum</i>	<i>Scabiosa ochroleuca</i>
<i>Astragalus spp.</i>	<i>Geranium pratense</i>	<i>Pastinaca sativa</i>	<i>Securigera varia</i>
<i>Bellis perennis</i>	<i>Gypsophila paniculata</i>	<i>Peucedanum oreoselinum</i>	<i>Senecio Jacobaea</i>
<i>Betonica officinalis</i>	<i>Hypericum spp.</i>	<i>Picris hieracioides</i>	<i>Sinapis arvensis</i>
<i>Calystegia sepium</i>	<i>Inula britannica</i>	<i>Pilosella officinarum</i>	<i>Solanum tuberosum</i>
<i>Campanula patula</i>	<i>Knautia arvensis</i>	<i>Plantago lanceolata</i>	<i>Sonchus arvensis</i>
<i>Carduus acanthoides</i>	<i>Lamium purpureum</i>	<i>Plantago media</i>	<i>Sonchus asper</i>
<i>Centaurea jacea</i>	<i>Lathyrus hirsutus</i>	<i>Potentilla arenaria</i>	<i>Stachys annua</i>
<i>Centaurea scabiosa</i>	<i>Lathyrus Pannonicus</i>	<i>Potentilla argentea</i>	<i>Stachys palustris</i>
<i>Centaurea spp.</i>	<i>Lathyrus pratensis</i>	<i>Potentilla erecta</i>	<i>Stachys recta</i>
<i>Centaurea stoebe</i>	<i>Lathyrus tuberosus</i>	<i>Potentilla reptans</i>	<i>Stellaria graminea</i>
<i>Cerintho minor</i>	<i>Leontodon hispidus</i>	<i>Prunella vulgaris</i>	<i>Stenactis annua</i>
<i>Cichorium intybus</i>	<i>Leontodon spp.</i>	<i>Prunella vulgaris</i>	<i>Symphytum officinale</i>
<i>Cirsium arvense</i>	<i>Leucanthemum vulgare</i>	<i>Pulicaria dysenterica</i>	<i>Taraxacum officinale</i>
<i>Convolvulus arvensis</i>	<i>Linum flavum</i>	<i>Ranunculus acris</i>	<i>Thymus praecox</i>
<i>Crataegus spp.</i>	<i>Linum spp.</i>	<i>Ranunculus bulbosus</i>	<i>Trifolium montanum</i>
<i>Crepis biennis</i>	<i>Lotus corniculatus</i>	<i>Ranunculus polyanthemos</i>	<i>Trifolium pratense</i>
<i>Cucurbita spp.</i>	<i>Lychmis flos-cuculi</i>	<i>Ranunculus repens</i>	<i>Trifolium repens</i>
<i>Cynoglossum officinale</i>	<i>Lythrum salicaria</i>	<i>Raphanus raphanistrum</i>	<i>Tripleurospermum inodorum</i>
<i>Daucus carota</i>	<i>Medicago falcata</i>	<i>Raphanus raphanistrum</i>	<i>Verbascum phoeniceum</i>
<i>Dorycnium herbaceum</i>	<i>Medicago lupulina</i>	<i>Rhinanthus minor</i>	<i>Veronica chamaedrys</i>
<i>Echium vulgare</i>	<i>Medicago sativa</i>	<i>Rhinanthus minor</i>	<i>Veronica teucrium</i>
<i>Eryngium campestre</i>	<i>Melilotus officinalis</i>	<i>Rhinanthus serotinus</i>	<i>Vicia pannonica</i>
<i>Euphorbia cyparissias</i>	<i>Mentha longifolia</i>	<i>Rhinanthus spp.</i>	<i>Vicia spp.</i>
<i>Falcaria vulgaris</i>	<i>Muscari tenuiflorum</i>	<i>Rorippa pyrenaica</i>	<i>Zea mays</i>
<i>Filipendula vulgaris</i>	<i>Myosotis spp.</i>	<i>Rorippa spp.</i>	

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777 **Appendix BC.** The names and abbreviations of the 133 pollinator species appearing in the
 778 studied plant-pollinator communities.

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Species	Abbreviation	Species	Abbreviation
<i>Andrena aeneiventris</i>	Andaen	<i>Halictus subauratus</i>	Halsub
<i>Andrena bicolor</i>	Andbic	<i>Heriades crenulatus</i>	Hercre
<i>Andrena dorsata</i>	Anddor	<i>Hoplitis leucomelana</i>	Hopleu
<i>Andrena flavipes</i>	Andfla	<i>Hylaeus angustatus</i>	Hylang
<i>Andrena fulvago</i>	Andful	<i>Hylaeus annularis</i>	Hylann
<i>Andrena gelriae</i>	Andgel	<i>Hylaeus brevicornis</i>	Hylbre
<i>Andrena hattorfiana</i>	Andhat	<i>Hylaeus communis</i>	Hylcom
<i>Andrena humilis</i>	Andhum	<i>Hylaeus confusus</i>	Hylcon
<i>Andrena labialis</i>	Andlas	<i>Hylaeus cornutus</i>	Hylcor
<i>Andrena labiata</i>	Andlab	<i>Hylaeus duckei</i>	Hylduc
<i>Andrena limata</i>	Andlim	<i>Hylaeus sinuatus</i>	Hylsin
<i>Andrena minutula</i>	Andmin	<i>Hylaeus variegatus</i>	Hylvar
<i>Andrena minutuloides</i>	Andmis	<i>Lasioglossum albipes</i>	Lasalb
<i>Andrena nitida</i>	Andnit	<i>Lasioglossum brevicorne</i>	Lasbre
<i>Andrena nitidiuscula</i>	Andnis	<i>Lasioglossum calceatum</i>	Lascal
<i>Andrena ovatula</i>	Andova	<i>Lasioglossum corvinum</i>	Lascor
<i>Andrena pallitarsis</i>	Andpal	<i>Lasioglossum costulatum</i>	Lascos
<i>Andrena pandellei</i>	Andpan	<i>Lasioglossum discum</i>	Lasdis
<i>Andrena polita</i>	Andpol	<i>Lasioglossum fulvicorne</i>	Lasful
<i>Andrena rosae</i>	Andros	<i>Lasioglossum glabriusculum</i>	Lasgla
<i>Andrena subopaca</i>	Andsub	<i>Lasioglossum griseolum</i>	Lasgri
<i>Andrena thoracica</i>	Andtho	<i>Lasioglossum interruptum</i>	Lasint
<i>Andrena ventricosa</i>	Andven	<i>Lasioglossum laevigatum</i>	Laslae
<i>Andrena viridescens</i>	Andvir	<i>Lasioglossum laticeps</i>	Laslas
<i>Andrena wilkella</i>	Andwil	<i>Lasioglossum lativentre</i>	Laslat
<i>Anthidium punctatum</i>	Antpun	<i>Lasioglossum leucozonium</i>	Lasleu
<i>Anthophora crinipes</i>	Antcri	<i>Lasioglossum lineare</i>	Laslin
<i>Anthophora furcata</i>	Antfur	<i>Lasioglossum lucidulum</i>	Lasluc
<i>Anthophora plumipes</i>	Antplu	<i>Lasioglossum majus</i>	Lasmaj
<i>Anthophora pubescens</i>	Antpub	<i>Lasioglossum malachurum</i>	Lasmal
<i>Apis mellifera</i>	Apimel	<i>Lasioglossum marginatum</i>	Lasmar
<i>Bombus hortorum</i>	Bomhor	<i>Lasioglossum morio</i>	Lasmor
<i>Bombus humilis</i>	Bomhum	<i>Lasioglossum nigripes</i>	Lasnig
<i>Bombus pascuorum</i>	Bompas	<i>Lasioglossum pauxillum</i>	Laspau
<i>Bombus pratorum</i>	Bompra	<i>Lasioglossum politum</i>	Laspol
<i>Bombus ruderarius</i>	Bomrud	<i>Lasioglossum punctatissimum</i>	Laspum
<i>Bombus sylvarum</i>	Bomsyl	<i>Lasioglossum puncticolle</i>	Laspun
<i>Bombus terrestris</i>	Bomter	<i>Lasioglossum truncaticolle</i>	Lastru
<i>Ceratina cyanea</i>	Cercya	<i>Lasioglossum villosulum</i>	Lasvil
<i>Ceratina nigrolabiata</i>	Cernig	<i>Lasioglossum xanthopus</i>	Lasxan
<i>Chelostoma florissomne</i>	Cheflo	<i>Lasioglossum zonulum</i>	Laszon
<i>Coelioxys afra</i>	Coeafr	<i>Megachile centuncularis</i>	Megcen
<i>Coelioxys mandibularis</i>	Coeman	<i>Megachile ericetorum</i>	Megeri
<i>Colletes daviesanus</i>	Coldav	<i>Megachile pilidens</i>	Megpil
<i>Colletes hylaeiformis</i>	Colhyl	<i>Megachile rotundata</i>	Megrot
<i>Colletes similis</i>	Colsim	<i>Melitta dimidiata</i>	Meldim
<i>Epeolus variegatus</i>	Epevar	<i>Melitta leporina</i>	Mellep
<i>Eucera chrysopyga</i>	Eucchr	<i>Melitta nigricans</i>	Melnig
<i>Eucera clypeata</i>	Euccly	<i>Melitturga clavicornis</i>	Melcla
<i>Eucera interrupta</i>	Eucint	<i>Nomada basalis</i>	Nombas
<i>Eucera longicornis</i>	Euclon	<i>Nomada pleurosticta</i>	Nomple
<i>Eucera nigrescens</i>	Eucnig	<i>Osmia bidentata</i>	Osmbid
<i>Halictus confusus</i>	Halcon	<i>Osmia leaiana</i>	Osmlea
<i>Halictus eurygnathus</i>	Haleur	<i>Osmia rufohirta</i>	Osmruf

<i>Halictus gavarnicus</i>	Halgav	<i>Osmia spinulosa</i>	Osmspi
<i>Halictus kessleri</i>	Halkes	<i>Osmia tergestensis</i>	Osmter
<i>Halictus langobardicus</i>	Hallan	<i>Panurgus calcaratus</i>	Pancal
<i>Halictus leucaheneus</i>	Halleu	<i>Pseudapis bispinosa</i>	Psebis
<i>Halictus maculatus</i>	Halmac	<i>Pseudapis diversipes</i>	Psediv
<i>Halictus patellatus</i>	Halpat	<i>Sphcodes ephippius</i>	Spheph
<i>Halictus rubicundus</i>	Halrub	<i>Sphcodes gibbus</i>	Sphgib
<i>Halictus scabiosae</i>	Halsca	<i>Sphcodes rufiventris</i>	Sphruf
<i>Halictus semitectus</i>	Halsem	<i>Systropha curvicornis</i>	Syscur
<i>Halictus sexcinctus</i>	Halsex	<i>Systropha planidens</i>	Syspla
<i>Halictus simplex</i>	Halsim	<i>Tetraloniella alticincta</i>	Tetalt
<i>Halictus smaragdulus</i>	Halsma	<i>Tetraloniella dentata</i>	Tetden
		<i>Tetraloniella salicariae</i>	Tetsal

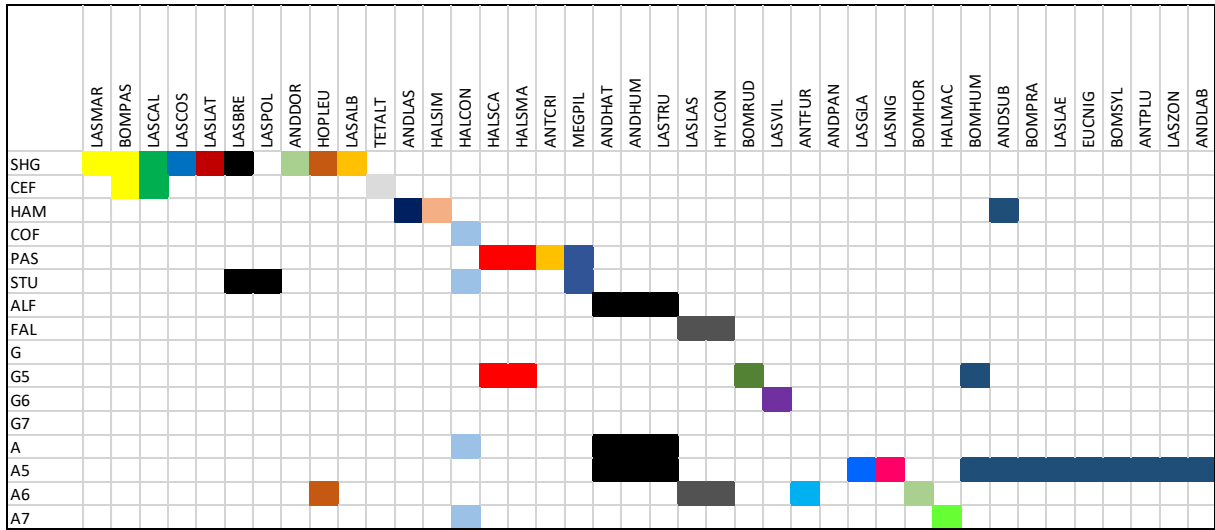
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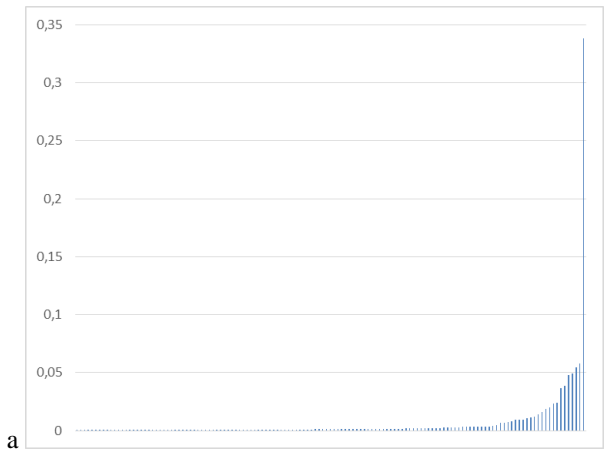
783 **Appendix ED.** Pollinators (in columns, see Appendix B-C for the codes) appearing in the
 784 dwarf components of the studied networks (in rows, see Table 1 for the codes). Since the STU
 785 network is very small, defining a "giant" component does not really make sense, so we show
 786 all pollinators here.

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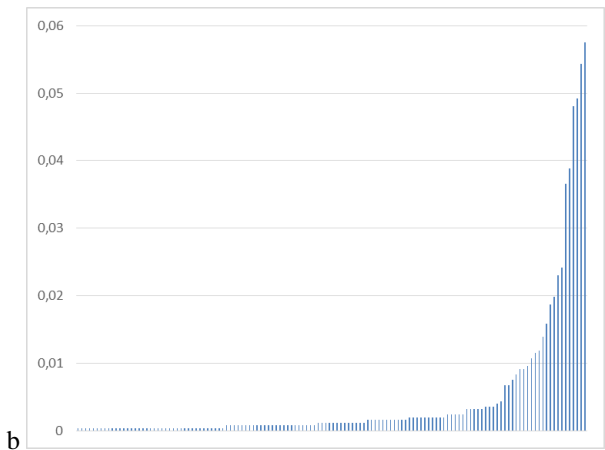


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792 **Appendix DE.** The rank of relative abundance values with (a) and without (b) the honeybee.
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