

1 **Small-scale agricultural landscapes and organic management support wild bee**
2 **communities of cereal field boundaries**

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18 **Abstract**

19 Pollinators are sensitive to agricultural intensification at both local and landscape scales. High
20 configurational landscape heterogeneity due to small fields and a high amount of field
21 boundaries is hypothesized to enhance farmland biodiversity. Here, we investigated the
22 effects of organic vs. conventional farming in large- vs. small-scale agricultural landscapes on
23 wild bee communities and their floral resources to improve conservation schemes for
24 pollinators. We sampled bees in Central Germany at the field boundaries of 18 pairs of
25 conventionally and organically managed winter wheat fields along the former iron curtain
26 using pan traps and trap nests. Around traps, we surveyed species richness and flower cover
27 of insect-pollinated forbs. Compared to conventional farming, organic farming was related to
28 higher insect-pollinated forb species richness and flower cover in the field boundaries,
29 presumably due to the lack of herbicide use. Interestingly, small-scale agriculture did not
30 counteract the loss of floral resources under conventional management, as the difference to
31 organic management was even larger in Western small-scale agriculture. Organic farming, but
32 not small-scale agriculture, enhanced species richness of solitary bees, which is in line with
33 their small home ranges. In contrast, bumblebees benefitted only from small-scale agriculture,
34 which matches with their high dispersal ability. Despite similar levels of abundance and
35 diversity of trap-nesting bees in the two landscape types, brood cell parasitism was also
36 higher in small-scale agriculture. Both organic farming and small-scale agriculture directly
37 and indirectly supported different groups of wild bees, suggesting long-term benefits for
38 conservation. Agri-environment schemes should acknowledge the so far neglected benefits of
39 small-scale agriculture for biodiversity and its potential services.

40

41 **Keywords:** Agri-environment schemes, insect-pollinated plants, landscape configuration, pan
42 trap, pollinators, trap nest

43

44 **1. Introduction**

45 Wild bees are strongly affected by agricultural intensification and landscape homogenization.
46 At the local scale, a major threat is the increased input of pesticides and fertilizers (Robinson
47 and Sutherland, 2002), whereas changes in the agricultural landscape due to increased field
48 sizes and the loss of suitable habitats exert pressure on biodiversity and ecosystem services
49 (Steffan-Dewenter et al., 2002; Tschardt et al., 2005; Rundlöf et al., 2008; Bommarco et al.,
50 2010). Declines in the abundance and diversity of native bees, and their services can be
51 explained by the isolation from critical floral and nesting resources (Steffan-Dewenter and
52 Tschardt, 1999; Kremen et al., 2002). Despite the importance of wild bees providing
53 pollination services and the increasing awareness of this problem (Klein et al., 2007; Aizen et
54 al., 2009; Garibaldi et al., 2013), pollinators in agricultural landscapes are still at risk.

55 Agri-environment schemes (AES) may be powerful mitigation tools to enhance habitat
56 quality for pollinators and combat biodiversity loss in intensively cultivated areas (Batáry et
57 al., 2015). Instead of establishing new protection areas, these schemes integrate conservation
58 efforts into the agricultural landscape. Farmers may provide flower strips, nesting resources
59 and restore semi-natural and natural areas adjacent to crops (Garibaldi et al., 2014, 2016;
60 Kleijn et al., 2015).

61 Even though AES are often considered as an expensive and complex form of
62 environmental protection (Batáry et al., 2015), the investment is observed to pay off. AES
63 enhance ecosystem services such as pollination and natural pest control by increasing
64 farmland heterogeneity and extensive farming practices (Inclán et al., 2015). Among AES
65 measures, organic farming is one of the most well-established management approaches
66 (Batáry et al., 2013). The high value of organic management for agro-biodiversity has been
67 shown for several agricultural systems (e.g. Schmidt et al., 2005; Rundlöf et al., 2008;
68 Schneider et al., 2014). Including data from 30 years and different farming systems in a meta-

69 analysis, Tuck et al. (2014) could show for example that organic farming increased species
70 richness by 30% with the strongest positive effects in cereals and mixed crops. Regarding
71 functional groups they emphasized the positive effect of organic farming on plants and
72 pollinators.

73 Various studies have shown that the composition of the surrounding landscape
74 moderates the effectiveness of AES in general, and organic farming in particular (Rundlöf et
75 al., 2007; Batáry et al., 2011). For example, pollinators profit from agri-environmental
76 management in simple but not in complex landscapes (Batáry et al., 2011). Landscape
77 configuration is an important factor affecting biodiversity and ecosystem services, but little is
78 known about how landscape configurational heterogeneity shapes biodiversity patterns under
79 AES (Belfrage et al., 2005; Marshall et al., 2006; Concepción et al., 2012). The shift from
80 small-scale family farms to large-scale agriculture has severely decreased landscape
81 configurational heterogeneity. This process is accompanied by a trend towards specialization
82 and the increase of field sizes on the expense of mixed farming and high quality edges, such
83 as hedgerows (Robinson and Sutherland, 2002; Holzschuh et al., 2010).

84 In this study, we used a novel approach to disentangle the interlinked effects of local
85 management and landscape configuration on wild bees. At the former inner German border
86 (iron curtain), two opposed farming strategies have led to diverging field size patterns. While
87 small private farms shape West Germany's agriculture, Eastern farms were merged and
88 organised in large cooperatives. In 1989, average farm size in the West was 18.17 ha. In East
89 Germany, farms were on average 250 times as large due to collectivisation under planned
90 economy (Koester, 1999). Similarly, in many Central and Eastern European countries,
91 collectivised family farms were merged to large industrial farms of several hundred or
92 thousand hectares in size (Davidova et al., 2012; Sutcliffe et al., 2015). Today, post-
93 communist legacy effects in the agricultural landscape are still visible and affect farmland

94 biodiversity (Báldi and Batáry, 2011; Konvicka et al., 2016; Batáry et al., 2017). We studied
95 the effects of farming practice and landscape configuration based on these historically grown
96 structures alongside the former iron curtain. Our research focused on wild bees, which
97 contribute crucially to ecosystem service provision in agricultural landscapes, and on insect-
98 pollinated forbs, which offer essential food resources for this prominent group of pollinators.
99 Both bees and forbs are highly sensitive indicators for agricultural intensification at the local
100 and the landscape scale, and thus belong to the major target groups of AES (Batáry et al.,
101 2015; Garibaldi et al., 2013; Kennedy et al., 2013). We expected local management and
102 landscape configuration to strongly affect abundance and species richness of both wild bees
103 and their floral resources in wheat field boundaries. We addressed the following research
104 questions: (1) Do insect-pollinated forb and wild bee species richness and abundance in cereal
105 field boundaries increase in small-scale compared to large-scale agricultural landscapes? (2)
106 Does organic farming enhance forb species richness and cover and pollinator diversity and
107 abundance? (3) Can we detect a coupled effect of farming practice and landscape
108 configuration on wild bees and their floral resources?

109

110 **2. Materials and methods**

111 *2.1. Study sites and study design*

112 We sampled a total of 36 winter wheat fields in southern Lower Saxony (former democratic
113 West Germany, hereafter ‘West’) and northern Thuringia (former communist German
114 Democratic Republic, hereafter ‘East’) in 2013, at both sides of the former inner German
115 border (Appendix S1 in Supplementary Material). Intensive cropland (mainly cereals and oil
116 seed rape) and pastures dominated the surrounding landscape accompanied by semi-natural
117 habitats such as forest patches and hedgerows. Annual precipitation was 581 mm and mean
118 annual temperature was 8.9 °C (measuring station Mühlhausen, 190 m a.s.l.) in Northern

119 Thuringia (DWD 2013). Western fields were situated around the city of Göttingen (weather
120 measuring station at 176 m a.s.l.) with a mean annual precipitation of 651 mm and a mean
121 annual temperature of 9.2 °C (DWD 2013). Edge length and average field size recorded in a
122 500 m buffer around study fields provided evidence for the strong contrast in landscape
123 configuration between large-scale East and small-scale West. Field edges in the West were
124 1.7 times longer and fields six times smaller than in the East), whereas the proportion of
125 agricultural area was similar in both landscape types (Table 1). The percentage of organic
126 farmland in the study regions accounted for 2.8% of the agricultural area in Lower Saxony
127 and 4.2% in Thuringia in 2015 (BMEL, 2015). We selected 18 pairs of organic and
128 conventional fields in both regions for simultaneous testing of the influence of landscape
129 configuration (large-scale East vs. small-scale West) and farming practice. In both regions,
130 conventional and organic systems were clearly differentiated based on management intensity
131 (no application of synthetic pesticides in organic farming; amount of nitrogen fertilizer used
132 about five times lower, and yields half as high in organic compared to conventional farming
133 (Batáry et al., 2017)). Fields belonging to one pair were located within the area of one village
134 in the immediate vicinity of each other (distance between paired fields in East: 2.60 ± 0.58
135 km; in West: 1.10 ± 0.22 km). Since organic farms are not as widely distributed in the East as
136 in the West, we had to apply a partly cross-nested study design (Batáry et al., 2017): In three
137 villages (in both East and West), we selected two pairs of fields belonging to the same
138 farmers, resulting in three villages with one pair and three villages with two pairs of organic
139 and conventional fields per landscape type (altogether 24 farms). On average, study field size
140 was seven times larger in the East than in the West (Table 1). Along each field, we selected
141 one grassy field boundary with homogeneous cover (excluding sown flower mixtures or
142 hedgerows) for pollinator sampling and vegetation surveys.

143

144 *2.2. Vegetation surveys*

145 Detailed vegetation surveys were conducted once in mid-June 2013, following the sampling
146 protocol used by Batáry et al. (2013). We assessed species richness and cover of insect-
147 pollinated forbs in three botanical plots of 5 × 1 m size, located in the centre of the grassy
148 field boundary and separated by 10 m from each other. Additionally, percent cover of
149 flowering plants, which might attract pollinators, was recorded in the plots around pan traps
150 (see below).

151

152 *2.3. Pollinator sampling*

153 In each field boundary, we sampled pollinators using three yellow pan traps placed on sticks
154 of 1 m height. We established the traps parallel to the field edge in the centre of the vegetation
155 survey plots at the field boundary. Yellow traps are known to be most attractive for wild bees
156 and are frequently used to compare pollinator diversity between different study sites (Grundel
157 et al., 2011; but see Morandin and Kremen, 2013). We opened the traps for seven days at each
158 site during three survey periods (May 6-16, May 28 - June 6 and June 24 - July 4, 2013).
159 Trapped pollinators were stored in 70% ethanol, dried, needled and identified to species level.

160 We sampled trap nesting bees using two trap nests per field boundary consisting of
161 plastic tubes filled with reed internodes (Gathmann et al., 1994). Each trap nest was
162 composed of two trapping cylinders set up on two wooden posts in 15 m distance from each
163 other in spring (April 22-24, 2014). We collected the traps in autumn (September 13-16,
164 2014). We opened occupied reed nests in the laboratory, examined them for parasitism and
165 identified trap-nesting bees and wasps to genus level.

166

167 *2.4. Statistical analyses*

168 We used the software R 3.3.2 (R Core Team, 2016) to conduct statistical analyses. We tested
169 the effects of farmland management and landscape configuration on insect-pollinated forb
170 diversity and cover, wild bee species richness and abundance (separately for solitary bees and
171 bumblebees) and genus richness, cell number and parasitized cell number of trap-nesting bees
172 and wasps by general and generalised linear mixed effect models (GLMM) using the
173 functions ‘lmer’ and ‘glmer’ of the package ‘lme4’ version 1.1-12 (Bates et al., 2015). To
174 avoid spatial and temporal autocorrelation, we pooled all samples per field by summing up
175 insect numbers. Based on the strong contrasts in landscape configuration and management
176 intensity (Table 1) we employed the factors ‘landscape scale’ (East: large-scale vs. West:
177 small-scale) and farm ‘management’ (organic vs. conventional) and their interaction as
178 categorical predictor variables. As some fields of the same management type belonged to the
179 same farmer, we included nested random effects, with ‘farmer’ nested in ‘village’ and ‘pair’
180 nested in ‘village’ (Batáry et al., 2017). In case of overdispersion, we accounted for
181 individual-level variability by including ‘field’ as additional random factor. We used visual
182 methods (quantile-quantile plots and homogeneity plots of residuals vs. fitted values) and
183 Shapiro-Wilk-tests to check the distribution of the residuals. Models were fitted with normal,
184 Poisson, or negative binomial distribution according to the error distribution of the response
185 variable (Table 2). We calculated all models nested in the global model by the command
186 ‘dredge’ in the package ‘MuMin’ version 1.16.4 (Barton, 2016) and compared them based on
187 Akaike Information Criterion corrected for small sample size (AICc). We performed model
188 averaging (Anderson and Burnham, 2002) if the top model and subsequent models differed
189 less than two units in AICc. Model-averaged parameter estimates were calculated over the
190 subset of models including the parameter (conditional average) to avoid shrinkage towards
191 zero (Grueber et al., 2011). We present the 95% confidence interval (CI) of parameter
192 estimates and the relative importance of each parameter. Relative importance is 0%, when the

193 parameter does not appear in the top model set, and reaches 100%, when the parameter is
194 present in all top models. Figures represent mean and standard error of the mean (SEM) of
195 species or genus richness and abundance, respectively, for each landscape and management
196 type.

197

198 **3. Results**

199 *3.1. Insect-pollinated forbs*

200 In total, we recorded 175 plant species in the cereal field boundaries. According to Klotz et al.
201 (2002), 70 of these species were insect-pollinated forbs (Table S1). Species richness of insect-
202 pollinated forbs was highest in organic field boundaries in both large-scale agriculture (43
203 species) and small-scale agriculture (47 species), whereas only 15 species were found in
204 conventional field boundaries in small-scale agriculture, compared to 37 species in large-scale
205 agriculture. For insect-pollinated forb species richness we retained the full model including
206 landscape scale, management, and the interaction term as single top model ($\Delta AICc < 2$).
207 There was an interaction between landscape scale and management, indicating a stronger
208 management effect on insect-pollinated forb species richness in small-scale agriculture than in
209 large-scale agriculture (Table 2, Fig. 1a). Forb cover differed between management types
210 (higher cover in organic than in conventional field boundaries), but not between landscape
211 scales, as the single best candidate model for insect-pollinated forb cover contained only
212 management as predictor variable (Fig. 1b).

213

214 *3.2. Bumblebees and solitary bees*

215 We collected a total of 1915 wild bees (1512 solitary and 403 social bees) using pan traps and
216 identified 81 species belonging to 16 genera (Table S2). The highest species richness and
217 abundance occurred within the taxon *Andrena* with the species *A. nigroaenea* and *A.*

218 *haemorrhoea* being the most frequent. Individuals of the managed European honeybee (*Apis*
219 *mellifera*) were excluded from the analyses.

220 Species richness and abundance of social wild bees, i.e. bumblebees, in field boundaries
221 depended on the landscape type (Table 2, Fig. 2a,c). However, the landscape effect on species
222 richness was less evident than on abundance, which was more than two times higher in small-
223 scale agriculture relative to large-scale agriculture. In contrast, species richness and
224 abundance of solitary bees were affected by management, but not by landscape scale (Fig.
225 2b,d). Again, the effect on abundance was stronger than on species richness, with the number
226 of solitary bees being reduced almost by one third under conventional compared to organic
227 management.

228

229 *3.3. Trap nesting bees and brood cell parasitism*

230 We found 13 genera of trap nesting bees and wasps checking 7126 brood cells. Overall,
231 3.21% of cells were parasitized (Table S3). Management was the only factor explaining genus
232 richness and cell number of trap nesting bees and wasps, but evidence for a positive effect of
233 organic management was limited (Table 2, Fig. 3a,b). However, there were about twice as
234 many parasitized cells in small-scale agriculture than in large-scale agriculture, and the single
235 best candidate model for the number of parasitized cells strongly supported an effect of
236 landscape scale (Fig. 3c).

237

238 **4. Discussion**

239 Based on differences in landscape configuration derived from opposing agricultural land-use
240 history in former East and West Germany, our study allowed disentangling landscape-scale
241 (large-scale vs. small-scale agriculture) and local (organic vs. conventional management)
242 effects on wild bee communities and their floral resources. Organic management consistently

243 increased the cover and species richness of insect-pollinated forbs in the cereal field
244 boundaries, in both large-scale and small-scale agricultural landscapes. However, the more
245 pronounced increase in forb species richness in small-scale agriculture compared to large-
246 scale agriculture suggested a higher effectiveness of organic management in small-scale
247 systems. The positive effect of organic management on forbs was accompanied by an
248 enhanced abundance of solitary wild bees. By contrast, bumblebee abundance did not increase
249 under organic management, whereas it was much higher in small-scale than in large-scale
250 systems. Similarly, parasitism of trap nesting bees and wasps was higher in the small-scale
251 than in the large-scale agriculture.

252

253 *4.1. Insect-pollinated forbs*

254 Forb species richness in field boundaries was notably reduced under conventional
255 management, particularly in small-scale agriculture. The decrease in diversity and cover of
256 forbs observed in landscapes characterized by high cover of conventionally managed arable
257 land has been explained by the intensive use of herbicides and the loss of semi-natural refuge
258 habitats (Roschewitz et al., 2005; Gaba et al., 2010; Dainese et al., 2016). Forb species
259 richness in field boundaries might also decrease with increasing fertilizer application in the
260 adjacent conventional crop field (Kleijn et al., 2009). In our study, there was no evidence that
261 conventional farmers applied higher amounts of fertilizers and pesticides in small-scale
262 compared to large-scale agriculture (Batáry et al. 2017). Given the similar level of agro-
263 chemical applications in both regions, we expected that higher edge lengths in small-scale
264 agriculture counteract habitat loss and enhance forb species richness and cover in
265 conventional field boundaries. In contrast, we found the difference in species richness and
266 cover of forbs between organic and conventional management to be much more pronounced
267 in small-scale than in large-scale agricultural landscapes. Consequently, in our study,

268 heterogeneous small-scale agriculture did not reduce the effectiveness of organic farming in
269 enhancing biodiversity, as suggested by other authors (Tscharntke et al., 2012). Based on our
270 experiences a tentative explanation could be that conventional field margins in the large-scale
271 agricultural landscapes in the East are less frequently managed by mowing compared to the
272 small-scale landscapes in the West (Chaudron et al., 2016).

273 Our findings substantiate strong benefits of organic farming for plant species richness
274 and cover, which are well-known and can be explained by the lack of herbicide application
275 (Roschewitz et al., 2005; Rundlöf et al., 2009; Tuck et al., 2014). Although the effectiveness
276 of organic farming has been questioned, for example in comparison to the restoration of semi-
277 natural habitats (Batáry et al., 2015), organic farming has generally been given credit for
278 balancing between multiple sustainability goals, such as productivity, environmental impact,
279 economic profit and human well-being (Reganold and Wachter, 2016).

280 It has been shown that the favourable effect of organic farming in terms of biodiversity
281 conservation increases in areas with high crop cover (Tuck et al., 2014; Batáry et al., 2015).
282 In our comparison of large-scale and small-scale farming systems, however, the proportion of
283 agricultural area covering the surroundings of our study sites was similar in both landscape
284 types (ca. 80%, Table 1). Thus we can largely exclude that differences in plant species
285 richness in organic field boundaries between small- and large-scale agriculture were related to
286 crop cover in the surrounding landscape.

287

288 *4.2. Bumblebees and solitary bees*

289 Our results provide evidence that organic farming succeeds not only in promoting
290 insect-pollinated forbs, but also solitary bee abundances in the wheat field boundaries. Social
291 bees, i.e. bumblebees, did not benefit from organic management but from small-scale
292 agriculture, indicating that bumblebees are more sensitive to landscape-scale intensification

293 than solitary bees. Larger body sizes in social bees translate to larger foraging ranges
294 (Westphal et al., 2006; Greenleaf et al., 2007; Kennedy et al., 2013), suggesting that social
295 bees perceive landscapes at a broader spatial scale than solitary bees (Steffan-Dewenter et al.,
296 2002). Steffan-Dewenter and Tschardtke (1999), who tested the effect of habitat isolation on
297 wild bees, confirmed a positive correlation of body size and foraging distance. In our study,
298 the large foraging ranges of bumblebees, especially of the most common species *Bombus*
299 *terrestris*, may partly explain the positive effect of landscape heterogeneity, i.e. smaller fields
300 with higher boundary lengths per unit area in small-scale agriculture, on bumblebee species
301 richness and abundance. Bumblebees depend strongly on high quality foraging habitat and
302 flower-rich field boundaries (Carvell et al., 2004), which were more available in small-scale
303 agriculture based on higher edge lengths (Table 1). Carvell et al. (2017), for instance, showed
304 that the survival of bumblebee family lineages between years increased significantly, when
305 bumblebees had access to flower rich field boundaries within 250-1,000 m from nesting sites.
306 Our finding that bumblebees benefit from small-scale agricultural landscapes is also in
307 accordance with Morandin et al. (2016), who showed that small-scale restorations of field
308 boundaries with hedgerows could be ecologically and economically cost effective in
309 promoting pollinators in adjacent crops within simplified agricultural landscapes.

310 Kennedy et al. (2013) found only weak effects of landscape configuration on wild bees,
311 but a strong influence of organic management. Contrary to our results, they reported that both
312 solitary and social bees profited from improved habitat conditions under organic management,
313 especially if vegetation diversity in the fields was high. There is no simple explanation why
314 the higher flower-richness we recorded in boundaries of organic fields did not lead to higher
315 bumblebee abundance and/or species richness. We assume that strong landscape-scale effects
316 in our study may have superimposed a potential positive effect of organic farming on
317 bumblebees. It is likely that the higher density of boundaries in small-scale agriculture offers

318 nesting sites and foraging resources at larger spatial scales, reducing the attractiveness of local
319 floral resources provided in organic field margins.

320

321 *4.3. Trap nesting bees and their parasitism*

322 Trap nest communities have been effectively used to study pollinators, predatory wasps, their
323 parasitoids and parasitism, which is an essential ecosystem function regulating host
324 populations (Tylianakis et al., 2006; Pereira-Peixoto et al., 2014, 2016). In our study,
325 parasitism of trap nesting bees and wasps was affected by small-scale agriculture, which
326 enhanced parasitoid abundance independently from farm management and host density.
327 Pereira-Peixoto et al. (2014) found more natural enemies of cavity-nesting bees in
328 heterogeneous habitats (urban-rural interface vs. either urban or rural), which were assumed
329 to provide more resources to parasitoids (Pereira-Peixoto et al., 2016), i.e. floral resources as
330 well as hosts and nesting sites for hosts. Their finding is in accordance with the high
331 parasitoid abundance we detected in small-scale agricultural landscapes, though we did not
332 find more brood cells of hosts or a higher number of cavity nesting bee genera in small-scale
333 agriculture. As opposed to this, Holzschuh et al. (2010) observed that local- and landscape-
334 scale effects on parasitoids were mainly mediated by their hosts, and parasitism rates were
335 marginally affected by local factors. However, in line with our findings, Steckel et al. (2014)
336 reported a similar response of trap nest parasitoids in grasslands at different land use
337 intensities, with parasitoids reacting more sensitive to low configurational landscape
338 heterogeneity than their hosts and perceiving the influence of this factor at larger spatial
339 scales (up to 1500 m). Hence, small-scale landscapes can enhance potential regulation of host
340 populations, which can be generally expected based on constraints in dispersal ability and
341 feeding specialization of natural enemies (Perović et al., 2017). By studying trap-nest
342 communities we were able to show that landscape configuration and management affect host

343 abundance and parasitism differently, implying effects on trophic interactions and ecosystem
344 functions.

345

346 **5. Conclusion**

347 Comparing management and landscape-scale effects on insect-pollinated forbs, bees and their
348 parasitoids, we showed that organic farming and the associated high availability of local floral
349 resources enhanced solitary bees, which are spatially restricted by their small foraging ranges.

350 Perceiving landscapes at a broader spatial scale, bumblebees profited from small-scale
351 agriculture. Therefore, we propose to promote small-scale agriculture, i.e. the reduction of
352 field sizes, as an AES to enhance habitat conditions for wild bee communities in farmland.

353 Next to organic management, the reduction of field sizes may serve as an effective tool to
354 support pollinators in the agricultural landscape.

355

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569 **Figure captions**

570

571 **Fig. 1.** Insect-pollinated forb species richness (a) and cover [%] (b) in boundaries of
572 conventionally and organically managed winter wheat fields in small-scale and large-scale
573 agricultural landscapes. Error bars represent SEM (n = 36).

574

575 **Fig. 2.** Bumble bee species richness (a) and abundance (c) and solitary bee species richness
576 (b) and abundance (d) in boundaries of conventionally and organically managed winter wheat
577 fields in small-scale and large-scale agricultural landscapes. Error bars represent SEM (n =
578 36).

579

580 **Fig. 3.** Genus richness (a) and cell number (b) of trap-nesting bees and number of parasitized
581 cells (c) in boundaries of conventionally and organically managed winter wheat fields in
582 small-scale and large-scale agricultural landscapes. Error bars represent SEM (n = 36).

583 **Table 1.** Local management intensity and landscape structure (in 500 m buffer) around study
 584 fields (n = 36 fields) in small (West) vs. large (East) scale agricultural systems with organic
 585 vs. conventional management (mean \pm SEM) during 2013 (based on Batáry et al. 2017)

	Small-scale agriculture (West)		Large-scale agriculture (East)	
	Organic	Conventional	Organic	Conventional
Local management				
Fertilizer (kg N/ha)	21.6 \pm 10.9	199.3 \pm 4.7	65.3 \pm 11.7	193.6 \pm 8.6
Pesticides (no. of appl.)	0.0 \pm 0.0	4.3 \pm 0.3	0.0 \pm 0.0	5.2 \pm 0.7
Study field size (ha)	3.0 \pm 0.5	3.1 \pm 0.3	21.8 \pm 3.6	20.0 \pm 3.0
Surrounding landscape				
Crop cover (%)	73.9 \pm 4.1	76.9 \pm 4.7	81.0 \pm 5.1	85.5 \pm 4.5
Edge length (km)	18.3 \pm 1.3	19.5 \pm 1.2	11.0 \pm 0.8	10.8 \pm 0.6
Field size (ha)	3.7 \pm 0.7	3.3 \pm 0.3	21.7 \pm 5.5	18.3 \pm 2.1

586

587 **Table 2.** Summary table for GLMM results after multimodel averaging of best candidate
 588 models showing relative importance of each explanatory variable (Management (M): organic
 589 vs. conventional; Landscape scale (L): large-scale vs. small-scale agriculture), its estimated
 590 effect on the response \pm 95% CI. Bold values indicate significant effect at $P = 0.05$

Model*	Variable	Relative importance (%) [†]	Multimodel estimate \pm 95% CI [‡]
Insect-pollinated forbs			
Species richness ²	Management	100	0.49 \pm 0.32
	Landscape scale	100	-0.70 \pm 0.64
	L \times M	100	0.89 \pm 0.54
Cover ¹	Management	100	0.19 \pm 0.10
Bumblebees			
Species richness ²	Landscape scale	66	0.38 \pm 0.39
Abundance ²	Landscape scale	100	1.07 \pm 0.58
Solitary bees			
Species richness ²	Management	54	0.18 \pm 0.20
Abundance ³	Management	33	0.30 \pm 0.04
Trap nesting bees and wasps			
Genus richness ²	Management	54	0.31 \pm 0.36
Cell number ³	Management	37	0.42 \pm 0.62
Parasitized cells ³	Landscape scale	100	1.02 \pm 0.92

*Models were fitted with normal (1), Poisson (2), or negative binomial distribution (3).

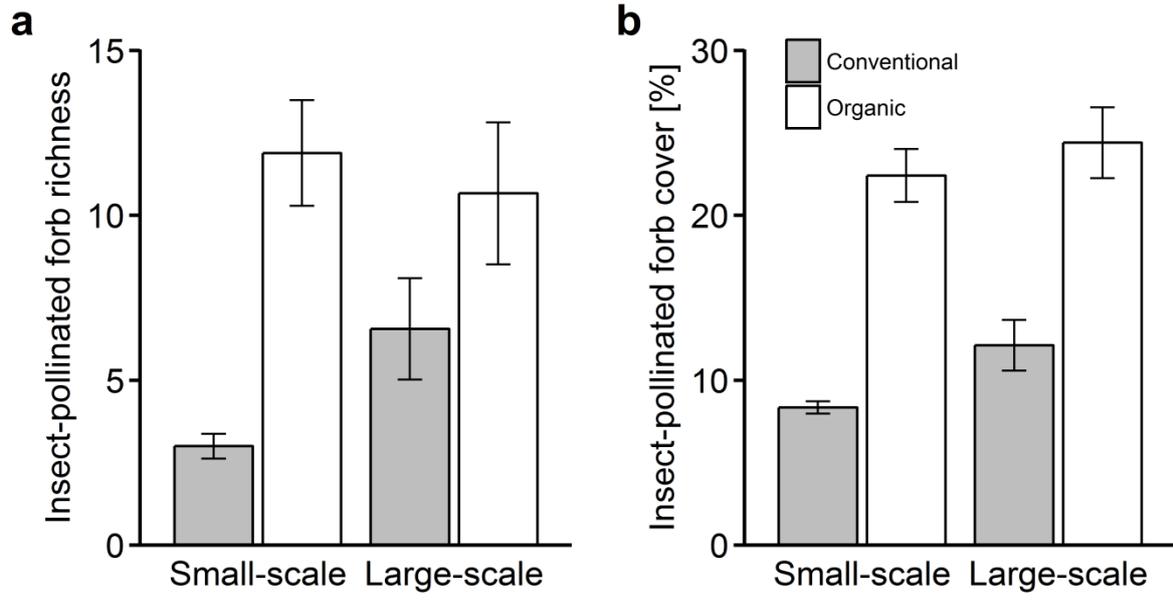
[†]Each variable's importance within the set of best candidate models ($\Delta AICc < 2$).

[‡]Estimates after multimodel averaging of the best candidate models ($\Delta AICc < 2$).

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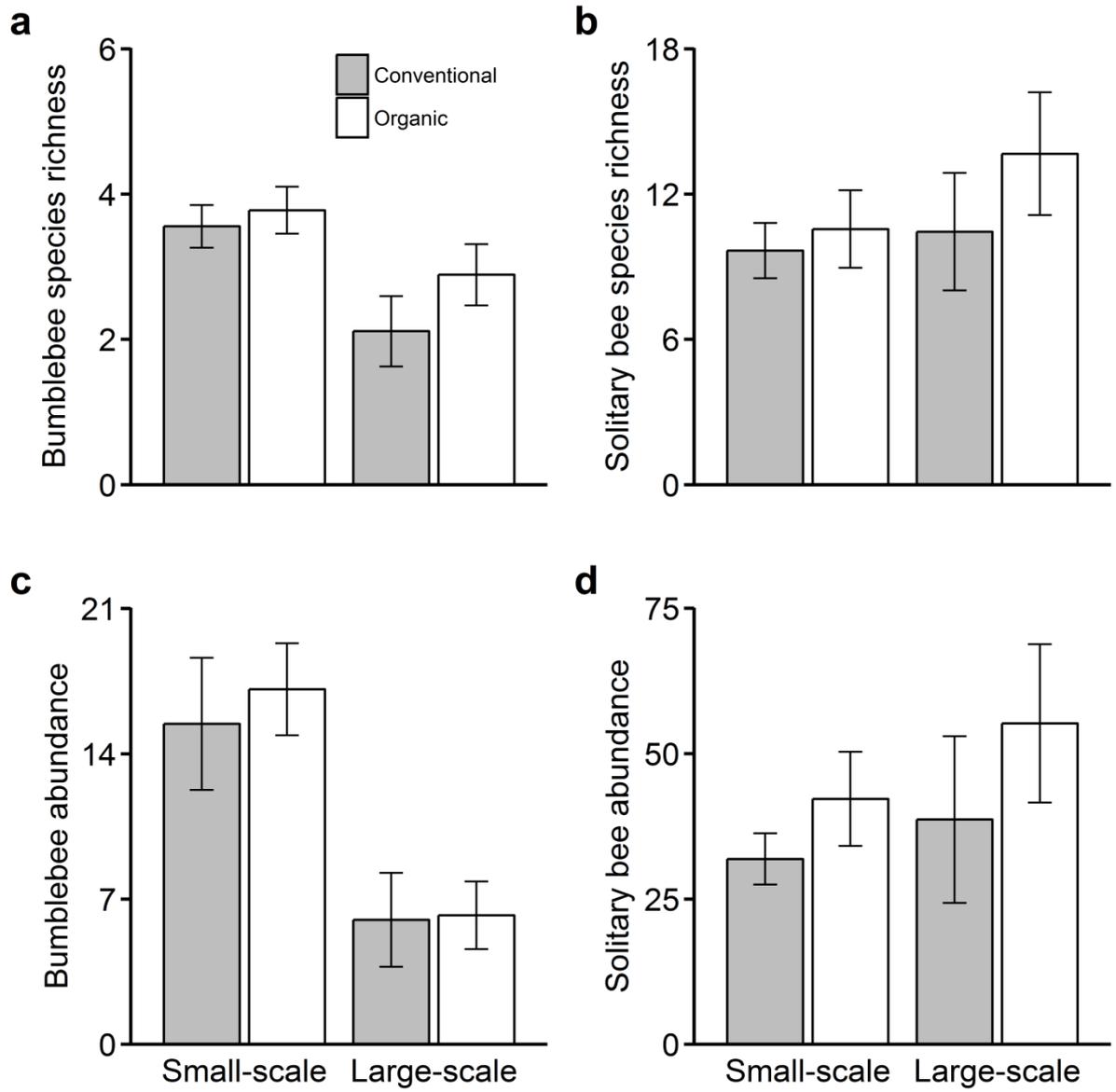
593 **Fig. 1.**



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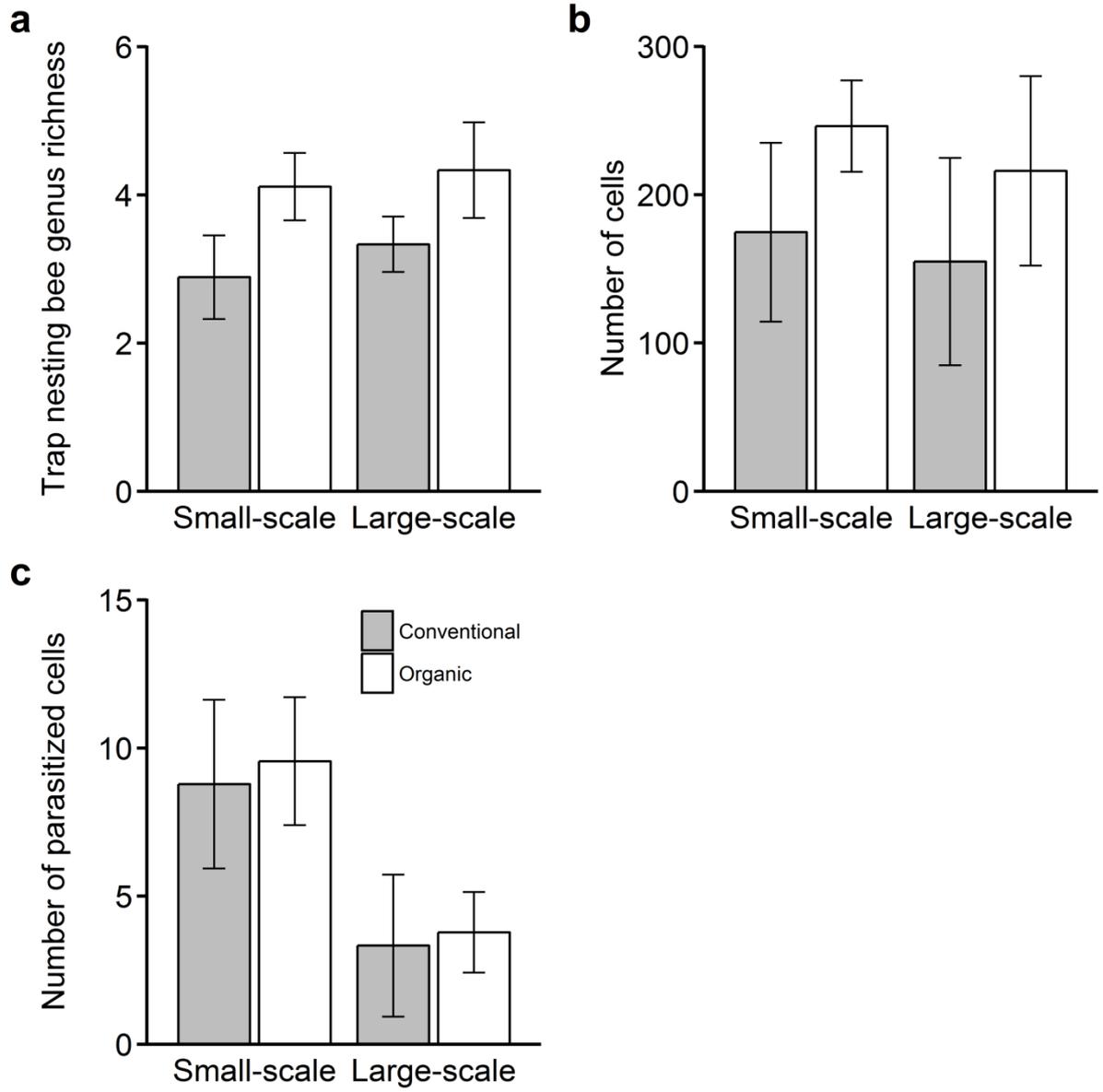
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596 **Fig. 2.**



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