

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

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## Abstract

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

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

## 1. Introduction

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

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

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

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

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

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

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

## **2. Materials and methods**

### *2.1. Study sites and study design*

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

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

## 2.2. *Vegetation surveys*

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

## 2.3. *Pollinator sampling*

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

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

## 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



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

### 3. Results

#### 3.1. *Insect-pollinated forbs*

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

#### 3.2. *Bumblebees and solitary bees*

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

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

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

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

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

## **4. Discussion**

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

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

#### *4.1. Insect-pollinated forbs*

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

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

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

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

#### *4.2. Bumblebees and solitary bees*

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

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

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

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

#### *4.3. Trap nesting bees and their parasitism*

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

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

## **5. Conclusion**

Comparing management and landscape-scale effects on insect-pollinated forbs, bees and their parasitoids, we showed that organic farming and the associated high availability of local floral resources enhanced solitary bees, which are spatially restricted by their small foraging ranges. Perceiving landscapes at a broader spatial scale, bumblebees profited from small-scale agriculture. Therefore, we propose to promote small-scale agriculture, i.e. the reduction of field sizes, as an AES to enhance habitat conditions for wild bee communities in farmland. Next to organic management, the reduction of field sizes may serve as an effective tool to support pollinators in the agricultural landscape.

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**Figure captions**

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

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

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

**Table 1.** Local management intensity and landscape structure (in 500 m buffer) around study fields (n = 36 fields) in small (West) vs. large (East) scale agricultural systems with organic 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

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

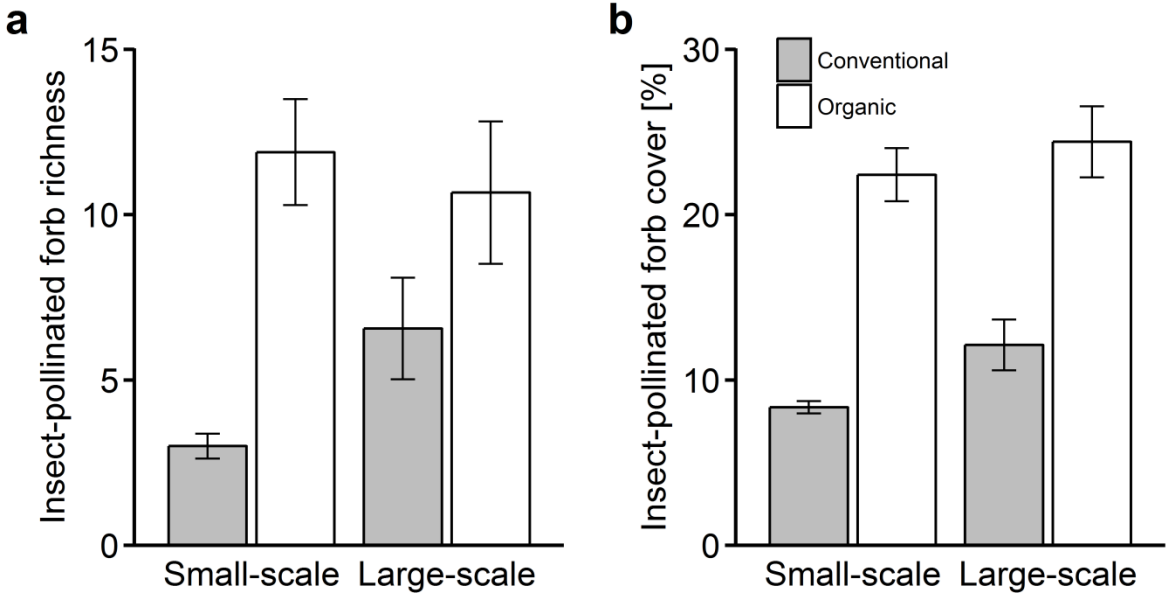
Model*	Variable	Relative importance (%) <sup>†</sup>	Multimodel estimate $\pm$ 95% CI <sup>‡</sup>
Insect-pollinated forbs			
Species richness <sup>2</sup>	Management	<b>100</b>	<b>0.49</b> $\pm$ <b>0.32</b>
	Landscape scale	<b>100</b>	<b>-0.70</b> $\pm$ <b>0.64</b>
	L $\times$ M	<b>100</b>	<b>0.89</b>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

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

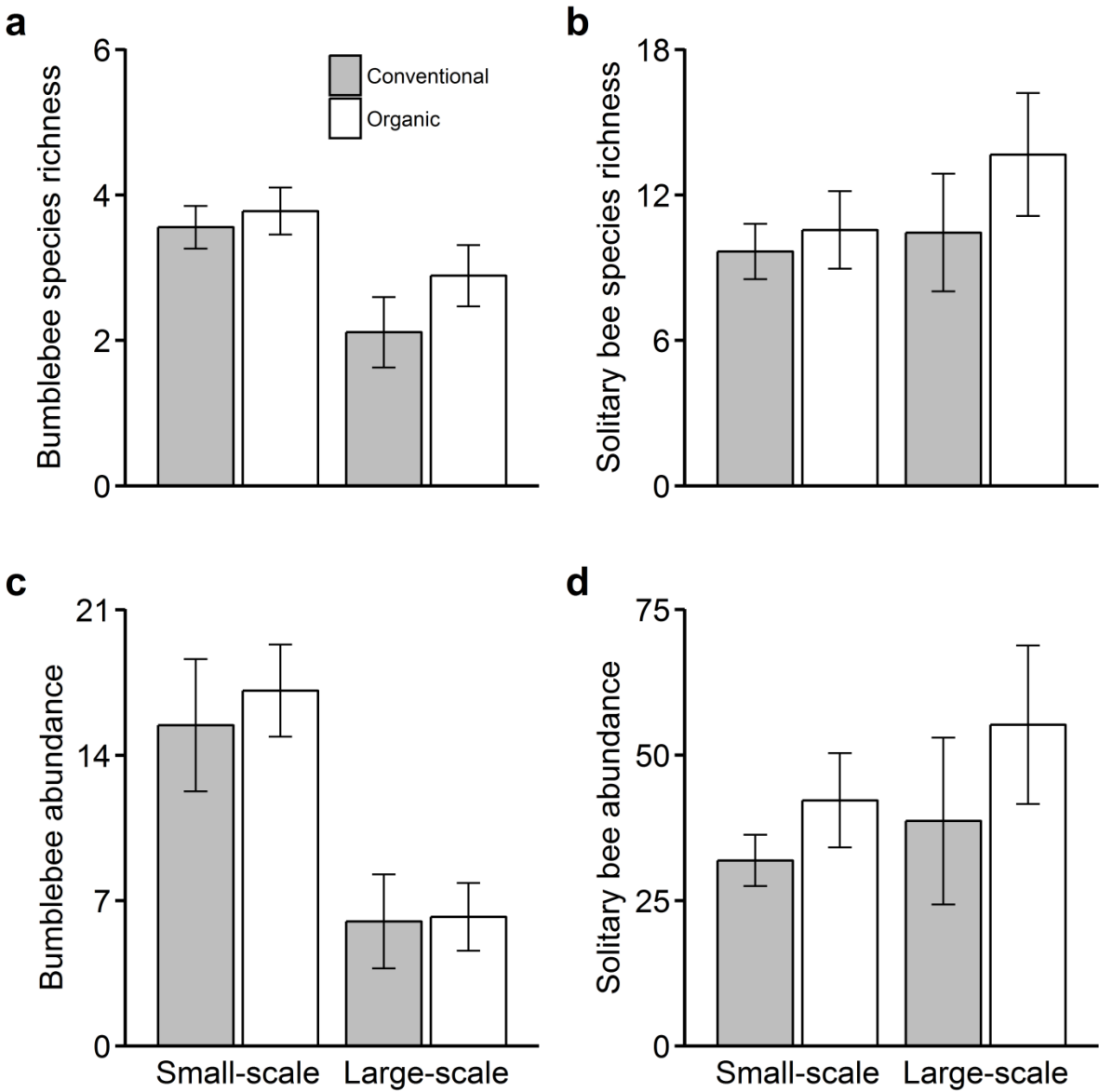
<sup>†</sup>Each variable's importance within the set of best candidate models ( $\Delta AICc < 2$ ).

<sup>‡</sup>Estimates after multimodel averaging of the best candidate models ( $\Delta AICc < 2$ ).

593 **Fig. 1.**



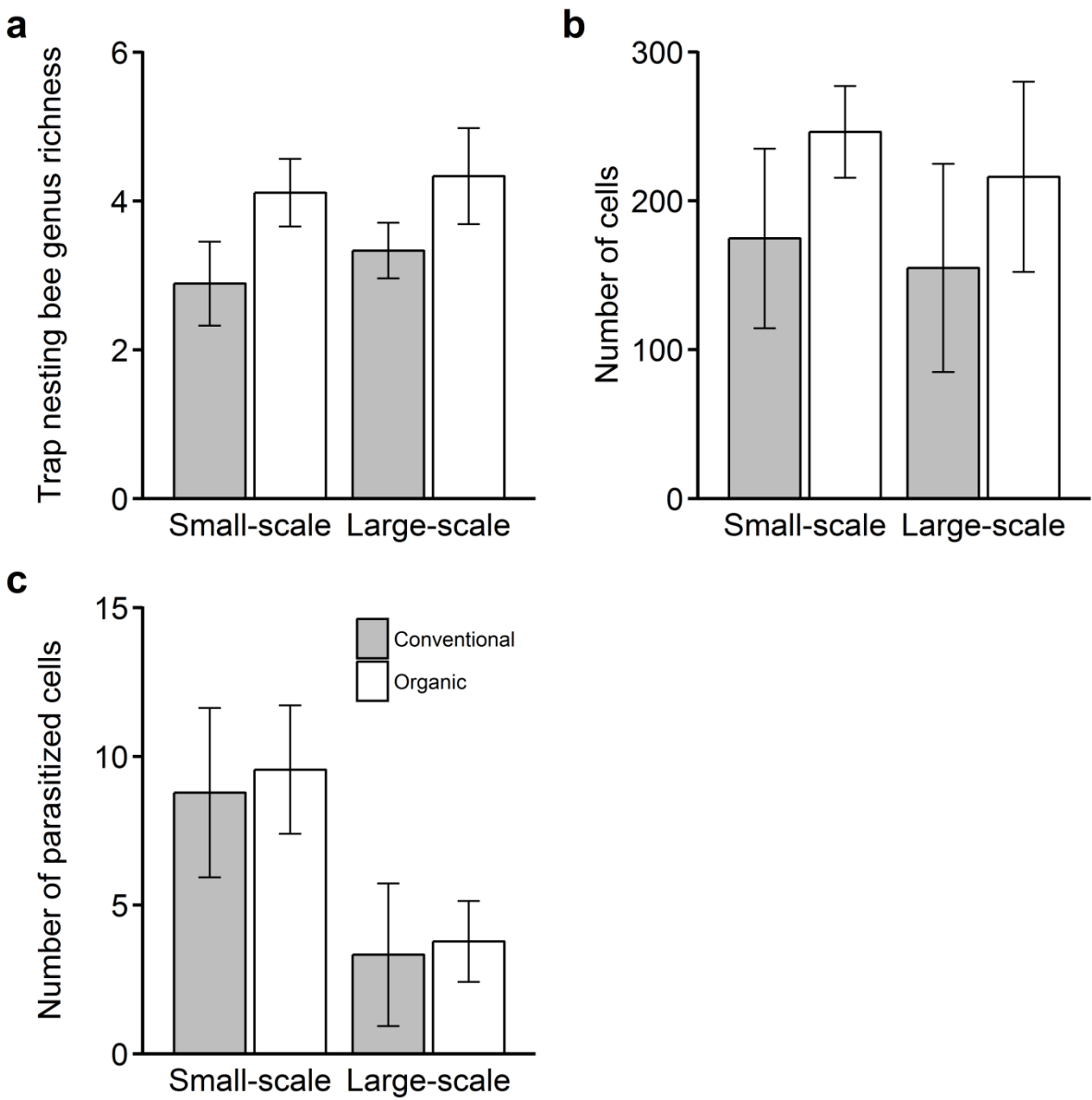
596 **Fig. 2.**



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599 **Fig. 3.**



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