

The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland

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Summary

1. Agri-environment schemes attempt to counteract the loss of biodiversity and associated ecosystem services such as pollination and natural pest control in agro-ecosystems. However, only a few studies have evaluated whether these attempts are successful.

2. We studied the effects of managing meadows according to the prescriptions of ecological compensation areas (ECA), the most widely adopted agri-environment scheme in Switzerland, on both pollinator species richness and abundance, and the reproductive success of plants in nearby intensively managed meadows (IM).

3. We established arrays of four pots, each containing individuals of three insect-pollinated, non-autogamous ‘phytometer’ species (*Raphanus sativus*, *Hypochaeris radicata* and *Campanula glomerata*), in ECA and adjacent IM at increasing distances from the ECA at 13 sites.

4. Species richness and abundance of hoverflies, solitary bees and large-sized pollinators (mainly social bees and butterflies) were significantly higher in ECA than in adjacent IM. Species richness and abundance of small-sized pollinators in IM declined significantly with increasing distance from ECA, whereas large-sized pollinators were not significantly affected by distance. Plant species richness and flower abundance were the major drivers of pollinator species richness and abundance; the area of an ECA had no significant influence.

5. Individual plants of *R. sativus* and *C. glomerata* produced more and heavier seeds in ECA than in IM. Furthermore, the number of seeds of these two phytometer species was positively correlated with species richness and abundance of bees. No such effects were observed for individual plants of *H. radicata*. The number of fruits and seeds per plant of *R. sativus* in IM decreased with increasing distance from ECA.

6. *Synthesis and applications.* We conclude that establishing ECA is an effective method of enhancing both pollinator species richness and abundance and pollination services to nearby intensively managed farmland. Our study emphasizes the importance of connectivity between ECA in maintaining diverse pollinator communities and thereby providing pollination services in agricultural landscapes.

Key-words: biodiversity, ecosystem functioning, habitat fragmentation, habitat quality, isolation distance, phytometer, pollinator guild, pollinator size, reproductive success

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Introduction

In the second half of the 20th century, the biodiversity within the European agricultural landscapes declined dramatically through intensification of agricultural practices coupled with habitat fragmentation (Saunders, Hobbs & Margules 1991; Robinson & Sutherland 2002). There is increasing concern that the loss of biological diversity has detrimental consequences for the functioning of ecosystems (Schlapfer & Schmid 1999; Loreau, Naeem & Inchausti 2002; Schlapfer, Pfisterer & Schmid 2005). In particular, ecosystem services provided to plants by animals, such as pollination and natural pest control, may be negatively affected before their dependence on the diversity of the faunal component is really understood (Kremen 2005). To counteract the loss of biological diversity and possible associated impairment of ecosystem services on farmland, agri-environment schemes have been implemented in most European countries since the early 1990s.

Agri-environment schemes are financial incentives that compensate farmers who apply management prescriptions to promote biodiversity (OECD 2003a). In Switzerland, farmers have received such direct payments for biodiversity management since 1993. From 1999 onwards, additional payments have been available for managing at least 7% of the farmland as ecological compensation areas (ECA) (Bundesrat 1998). ECA consist of a variety of specifically defined biotopes, such as wildflower strips, orchards, hedges and extensively managed hay meadows. In 2003, ECA covered 13% of the cultivated area of Switzerland (Herzog *et al.* 2005). As approximately 80% of the Swiss agricultural area is grassland, ECA hay meadows constitute by far the most widespread type of ECA, at 78% in 2004 (BLW 2004). Postponed mowing (after 15 June in the Swiss lowland) and prohibition of fertilizer application are the major management prescriptions for ECA hay meadows (Bundesrat 1998) (hereafter, ECA stands for ECA hay meadows).

In 2003, the agri-environmental budget was estimated at 2.2 billion euros for the European Union (EU) member states and 2.0 billion US dollars for the USA (OECD 2003b). However, despite these economic costs, few studies have evaluated the consequences of agri-environment schemes on biodiversity (Kleijn *et al.* 2001; Kleijn & Sutherland 2003; Herzog *et al.* 2005; Knop *et al.* 2006). In particular, we need to know whether the beneficial effects of agri-environment schemes on biodiversity also result in a more efficient provision of ecosystem services, as this would have positive economic consequences (Kremen, Williams & Thorp 2002). There is concern that the world-wide declines of pollinators will disrupt essential plant–pollinator interactions (Kearns, Inouye & Waser 1998) and thus also have negative economic consequences (Myers 1996; Ricketts *et al.* 2004).

Recent work has revealed the prominent role of natural habitat as a source of arthropod diversity in

agricultural landscapes (Duelli & Obrist 2003). However, few studies have investigated the effects of these source habitats on pollinator species richness and abundance and on their pollination services in adjacent agricultural land (Steffan-Dewenter & Tschardt 1999; Kremen, Williams & Thorp 2002; Klein, Steffan-Dewenter & Tschardt 2003a; Ricketts *et al.* 2004; Blanche & Cunningham 2005). This is also true for ECA, which should provide pollination services to adjacent intensively used land (Kremen, Williams & Thorp 2002; Ricketts *et al.* 2004). The present study aimed to define key factors for the effectiveness of ECA, for example the quality of floral resources, size and connectedness (Kremen *et al.* 2004; Kremen 2005), and evaluate pollinator services in adjacent intensively managed meadows (IM).

We addressed the following questions. (i) Do ECA have higher pollinator species richness and abundance than IM, and do the size, age and plant diversity of ECA influence these pollinator variables? (ii) Are pollinator richness and abundance in IM negatively correlated with distance from ECA and do different pollinator guilds show differential declines with distance? (iii) Is the reproductive success of target plants higher in ECA than in IM and does it decline with distance from ECA? (iv) Can a reduced reproductive success of target plants be explained by reduced pollinator richness and abundance?

Materials and methods

STUDY SITE AND EXPERIMENTAL DESIGN

The field experiment was conducted between May and September 2004, in the south-eastern part of the canton of Aargau, near Zurich, Switzerland. The region represents a Swiss lowland area of intensively managed agricultural landscape, consisting of a small-scale mosaic of grasslands, arable fields and forests. Thirteen pairs of ECA, ranging in size from 0.48 ha to 2.15 ha, and adjacent IM were selected. Each pair within a site had the same exposure and slope, and no other semi-natural habitats or other ECA occurred within 200 m of the pair. All ECA had been under the agri-environment scheme for at least 5 years and met the minimum ecological quality standard for vegetation (> 5 plant species listed as indicators under Swiss law on the ecological quality of ECA; BLW 2001).

In total, 56 experimental arrays of target plants, each consisting of four pots, were set up. At each of the 13 study sites, one array (hereafter station) was placed in the centre of the selected ECA. In the adjacent IM, stations were established at increasing distances of 25 m, 50 m, 100 m and, at four study sites, at 200 m from the nearest border of the ECA. The pots of each station were arranged in a line parallel to the ECA–IM border with 0.5-m gaps between pots. To assess the relevant spatial scale for the experiment, we calculated the distance between all 319 ECA in our study area from

their nearest neighbouring ECA to the north, east, south and west. The mean distance among ECA was 264.2 ± 6.6 m (225.8 m– 321.9 m), resulting in an average half distance between two neighbouring ECA of 132.1 m.

Each of the four pots per station contained an individual plant of radish *Raphanus sativus* L., one of clustered bellflower *Campanula glomerata* L. and one of common catsear *Hypochaeris radicata* L., resulting in four individuals of each target plant species at each station. None of the three phytometer species occurred naturally within a perimeter of 500 m around the stations at any of the 13 study sites. As all three phytometer species are obligate out-crossers, relying on insects for pollination, differences in the reproductive success of a phytometer species between stations should result only from differences in pollinator abundance and diversity between stations. The possibility for pollen exchange between plants among different stations was minimized by placing individual stations at least 50 m apart.

To examine the influence of the vegetation on species richness and abundance of pollinators, all plant species were mapped between May and June 2004 within five 2×5 -m strips arranged on both sides of each station at an interval of 2.5 m and parallel to the border of the ECA. In addition, flower abundance was estimated during two survey rounds in May and June/July as the area covered by herbs and the percentage with open flowers per plot, averaged over the five plots and the two survey rounds.

PHYTOMETER SPECIES

Raphanus sativus (Brassicaceae) is a weedy annual whereas *C. glomerata* (Campanulaceae) and *H. radicata* (Asteraceae) are perennial herbs. For *R. sativus* and *H. radicata*, a high degree of self-incompatibility is confirmed (Young & Stanton 1990; Pico, Ouborg & Van Groenendael 2004). *Campanula glomerata* is protogynous and probably self-incompatible (Blionis & Vokou 2005). To prove the dependence on pollinators for successful pollination of this species, we bagged several flower buds per station with fine gauze 1–7 days before flowers opened. To minimize microclimatic differences between bagged and open flowers, bagged flowers were checked weekly and bags were removed if flowers were withered unambiguously (Dafni 1992). The mean number of seeds per fruit of bagged flowers was 0.12 ± 0.05 ($n = 142$ fruits) compared with a mean number of seeds per fruit of 50.75 ± 1.71 ($n = 455$ fruits) of unbagged flowers, confirming a high degree of self-incompatibility in this species.

Seeds of the phytometer species were sown into pots (3-L, 20-cm diameter) filled with commercial standard garden soil, and placed in a glasshouse. *Campanula glomerata* and *H. radicata* seeds were sown on 18 September 2003, and *R. sativus* seeds on 5 March 2004. On 12–15 May three seedlings, representing the three

phytometer species, were transplanted into single pots, which were kept in a pollinator-free glasshouse until 24–25 May, when they were moved to the field. Pots were placed into holes in the ground so that phytometer plants were at a natural vegetation height. All experimental plants were watered at least weekly, more frequently if required.

POLLINATOR VISITATION

Flower-visiting insects were collected on each phytometer species throughout flowering time, which lasted from 1 June to 14 September 2004. To record abundance and identity of floral visitors, each station was sampled for 20 min between 10:00 and 16:00 h in sunny weather conditions with low wind velocity during three observation rounds (May, July, August). Only insects that landed on open flowers were considered as visitors, and these were sampled immediately after landing with a sweep-net. Sampled insects were transported in cooled plastic bags, kept frozen and identified in the laboratory. All individuals of the three most important pollinator taxa, bees (Hymenoptera: Apoidea), hoverflies (Diptera: Syrphidae) and butterflies (Lepidoptera: Diurna), were determined to species level. Pollinator taxa were grouped into large (i.e. body length = 12 mm; butterflies, bumblebees *Apis mellifera* L. and the hoverflies *Eristalis tenax* L. and *Scaeva pyrastris* L.) and small (body length < 12 mm; solitary bees, wasps, beetles and all flies other than the two large hoverfly species) body-size guilds, as we expected these two guilds to differ in their response to increasing distance from ECA.

PLANT REPRODUCTIVE SUCCESS

Plants of *R. sativus* were harvested between 20 and 22 September. Plants of *C. glomerata* and *H. radicata* were checked regularly for ripe fruits, which were harvested continuously. Developing capitula of *C. glomerata* and *H. radicata* were also bagged with fine mesh gauze to prevent loss of ripe seeds. Of 672 potted plants, 58 (8.6%) were damaged by agricultural machines, herbivorous mammals or severe weather (hail) and had to be omitted from the analyses. To estimate plant reproductive success, we counted the number of seeds in 50 fruits per individual of *R. sativus*, four fruits per individual of *C. glomerata* and two capitula per individual of *H. radicata*. Seeds were weighed after drying for 24 h at 65 °C. For *R. sativus*, we also determined the proportion of flowers that developed into fruits. Damaged and predated fruits and capitula were not used in the analyses of the numbers of seeds and seed mass.

PRE-DISPERSAL FRUIT PREDATION

All fruits of *R. sativus* ($n = 8621$) were stored for 1 month in the laboratory in plastic tubes closed with

Table 1. Flower-visiting insects captured during 56 h of sample time on *R. sativus*, *H. radicata*, *C. glomerata* and all three plant species together. n_i , number of individuals; n_s , number of species

Pollinator group	<i>R. sativus</i>		<i>C. glomerata</i>		<i>H. radicata</i>		All species	
	n_i	n_s	n_i	n_s	n_i	n_s	n_i	n_s
All bees (Apoidea)	47	16	44	13	65	16	156	31
<i>Apis mellifera</i> L.	3	1	8	1	9	1	20	1
Solitary bees	42	13	16	9	53	12	111	26
Bumblebees	2	2	20	3	3	3	25	4
Other Aculeata	5		1		15		21	
Hoverflies (Syrphidae)	107	13	146	17	388	19	641	25
Other Diptera	40		26		46		112	
Butterflies (Lepidoptera)	2	1	5	3	6	4	13	5
Beetles (Coleoptera)	3	1	1	5				
Small-sized pollinators	224		181		443		848	
Large-sized pollinators	27	7	44	9	77	10	147	12
All pollinators	250		225		520		995	

gauze and subsequently kept at -20°C in a freezer. A fruit was classified as attacked by herbivores if it contained larvae or imagines of insects inside the seeds or fruits, or if fruits unambiguously exhibited signs of herbivory, such as holes and hollowed seeds. Seed-predating insects were primarily larvae of bruchid beetles, tephritid flies and Microlepidoptera.

STATISTICAL ANALYSIS

To analyse variation in species richness and abundance of pollinators, we fitted general linear models with site, station within site, pot within station and plant within pot as blocking factors (block/plot/subplot/subject structure) and distance \times phytometer species \times date (three sampling rounds) as treatment factors. Distance was decomposed into contrast ECA vs. IM (management contrast, corresponding to 0 m vs. > 0 m distance from ECA), a log-distance contrast (increasing distance within IM; explaining greater amounts of variation than the alternative linear contrast) and the remaining deviation from log-linearity (within IM). Pollinator variables were also analysed separately for each phytometer species. The habitat covariates plant species richness, flower abundance, ECA size and ECA age were entered into the statistical model before the distance contrasts. To analyse the influence of ECA management and distance on plant reproduction (and the rate of pre-dispersal seed predation in *R. sativus*), the general linear model was fitted for each phytometer species separately without date as treatment factor. The relationship between species richness and abundance of the different pollinator guilds and plant reproduction was assessed at the station level using simple linear regression. All statistical analyses were done in R (R Development Core Team 2004). Response variables were square-root transformed if this improved normality and homoscedasticity (species richness and abundance of each tested pollinator group) and arcsine square-root transformed if they were proportions (fruit/flower ratio in *R. sativus*; Quinn & Keough 2002).

Results

FLOWER-VISITING INSECTS

We collected 250 flower-visiting insects on *R. sativus*, 225 on *C. glomerata* and 520 on *H. radicata* (Table 1). Hoverflies were by far the most abundant. However, species richness was comparably high for bees and hoverflies. Butterfly visits were rare. Small-sized pollinators accounted for 89.2% of the visits on *R. sativus*, 85.2% on *H. radicata* and 80.4% on *C. glomerata*. A rarefaction procedure (Duelli, Obrist & Schmatz 1999) showed that species saturation was similar in ECA (92.8%) and IM (93.6%). Species richness and abundance were highly correlated ($R^2 = 0.69$, $P = 0.001$) and decreased significantly during the sampling period from May to August within each pollinator group (species richness, $F_{1,15} = 6.40$, $P = 0.01$; abundance, $F_{1,15} = 9.37$, $P = 0.002$).

Because species richness and abundance were low in bumblebees, honeybees and butterflies, these three large-sized pollinator groups were pooled in further analyses (the general pattern found by the separate analyses was congruent with that of the pooled data). Further pooling across the three phytometer species showed that species richness and abundance of these large-sized pollinators, but also of solitary bees and hoverflies, were significantly higher in ECA than in IM (Table 2). This pattern was consistent over the 13 study sites except for solitary bees, for which significant site-management interactions for abundance ($F_{1,15} = 4.06$, $P = 0.006$) and species richness ($F_{1,15} = 3.80$, $P = 0.009$) were found. Species richness and abundance of solitary bees and hoverflies in IM declined significantly with increasing distance from ECA, paralleled by significant declines in Apoidea, small-sized pollinators and the total number of pollinators (Table 2). In contrast, there was no significant effect of distance on abundance or species richness of the large-sized pollinators. There were significant differences between phytometer species in the species composition of pollinators, but the general pattern of effects found in the separate analysis

Table 2. Summary of nested ANOVAS testing the effects of management (contrast: ECA vs. IM) and distance (contrast: log-distance from ECA within IM) on species richness and abundance of pollinator groups per 60 min of sample time (square-root transformed) at the level of the pot station (pooled data of all three phytometer species). Small-sized pollinators: mainly flies (except two large hoverfly species) and solitary bees. Large-sized pollinators: bumblebees, honeybees, butterflies and two large hoverfly species (see the Materials and methods). Significant statistics are shown in bold.

		Management		Distance	
Pollinator group	d.f.	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Species richness					
All bees (Apoidea)	1,15	49.85	< 0.001	9.29	0.008
Solitary bees	1,15	25.08	< 0.001	14.48	0.002
Hoverflies (Syrphidae)	1,15	9.05	0.009	8.96	0.009
Small-sized pollinators	1,15	44.49	< 0.001	13.58	0.002
Large-sized pollinators	1,15	32.57	< 0.001	1.85	0.194
All pollinators	1,15	56.72	< 0.001	12.33	0.003
Abundance					
All bees (Apoidea)	1,15	50.75	< 0.001	10.92	0.005
Solitary bees	1,15	22.44	< 0.001	15.52	< 0.001
Hoverflies (Syrphidae)	1,15	22.25	< 0.001	9.58	0.007
Small-sized pollinators	1,15	61.53	< 0.001	21.92	< 0.001
Large-sized pollinators	1,15	47.20	< 0.001	1.95	0.183
All pollinators	1,15	62.68	< 0.001	18.89	< 0.001

of the three phytometer species did not differ markedly from that of the pooled data (results therefore not shown). Species richness and abundance of solitary bees and hoverflies in IM declined significantly with log-distance from ECA, indicating that these variables followed negative exponential functions, with solitary bees showing a more pronounced decline than hoverflies (Fig. 1a,b). Large-size pollinators did not show these declines in IM with increasing distance from ECA (Fig. 1c and Table 2).

The habitat covariate plant species richness had a significant positive effect on both species richness and abundance of all collected pollinator groups (Table 3). For hoverflies, the habitat covariate flower abundance had an even stronger positive influence, whereas the positive effect on solitary bees was marginal. ECA age had a significant positive effect on species richness and abundance of solitary bees and Apoidea. Plant species richness and flower abundance explained a large part of the management contrast between ECA and IM, which was no longer significant (except for a marginal significance for the species richness of solitary bees and hoverflies) in the analyses with the habitat covariates, whereas the log-distance contrast remained significant (or marginally significant for the species richness of hoverflies) (Table 3). This indicated that, primarily, the increased plant species richness and flower abundance of ECA accounted for higher richness and abundance of pollinators in ECA than IM.

PLANT REPRODUCTIVE SUCCESS

Plants of *R. sativus* and *C. glomerata* produced more and slightly heavier seeds in ECA than IM (Table 4). However, management did not affect reproduction

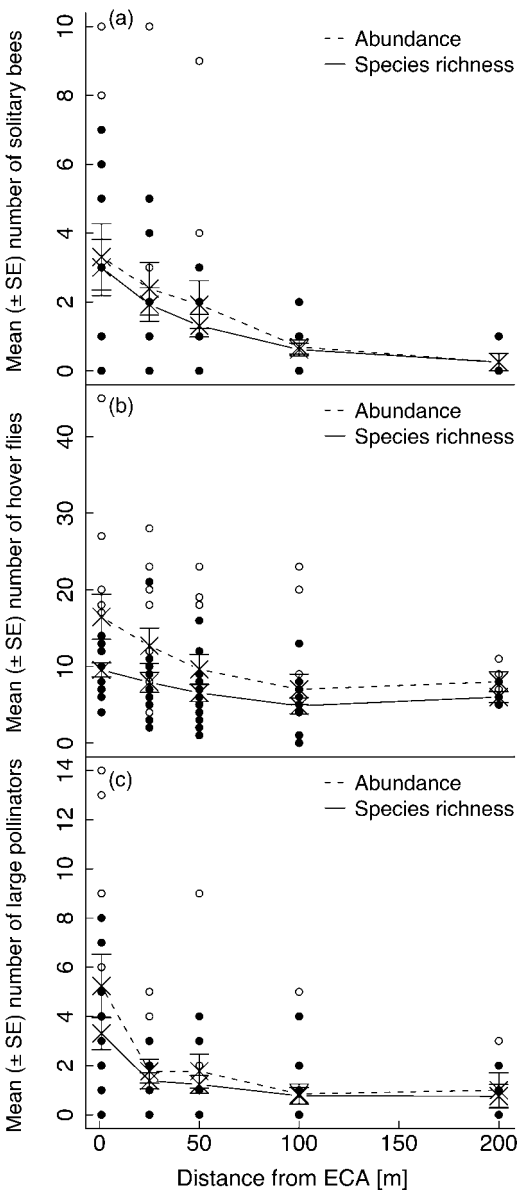


Fig. 1. Mean (± 1 SE) species richness and mean (± 1 SE) abundance of (a) solitary bees, (b) hoverflies and (c) large-sized pollinators on three species of phytometers in ECA (0 m) and at distances of 25 m, 50 m, 100 m ($n = 13$) and 200 m ($n = 4$) from the ECA within IM. Untransformed, pooled data of the three phytometer species are shown.

of the third phytometer species, *H. radicata*. There was a tendency for reduced fruit set and seed number of *R. sativus* (Fig. 2a) and increased seed mass of *H. radicata* with increasing distance from ECA.

Number of fruits and seeds per plant and seed mass of *R. sativus* increased linearly with species richness and abundance of solitary bees, Apoidea and small-sized pollinators (Table 5 and Fig. 2b). Seed numbers of *C. glomerata* increased linearly with species richness and abundance of solitary bees, Apoidea and large pollinators. The seed mass of this species was marginally positively correlated with the abundance of small pollinators. Reproductive traits of plants of *H. radicata* were not related to richness and abundance of pollinators.

Table 3. Summary of nested ANOVAS testing for the effects of the covariates plant species richness, flower abundance (tested at the station level), age of ECA and size of ECA (tested at the level of the study site) on species richness and abundance of pollinator groups (square-root transformed) per 60 min of sample time (pooled data of all three phytometer species). Effects on management (contrast: ECA vs. IM) and distance (contrast: log-distance from ECA within the IM) are given, when the covariates plant species richness and flower abundance were entered in the model before the contrasts management and log-distance. Small-sized pollinators: mainly flies (except two large hoverfly species) and solitary bees. Large-sized pollinators: bumblebees, honeybees, butterflies and two large hoverfly species (see the Materials and methods). Significant statistics shown in bold.

		Plant species richness		Flower abundance		Management		Distance			ECA age		ECA size	
Pollinator group	d.f.	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Species richness														
All bees (Apoidea)	1,13	27.81	< 0.001	10.61	0.005	8.53	0.012	8.24	0.013	1,11	9.48	0.011	0.01	0.919
Solitary bees	1,13	16.46	0.001	3.88	0.069	4.16	0.062	11.95	0.004	1,11	7.55	0.003	0.10	0.758
Hoverflies (Syrphidae)	1,13	5.61	0.033	8.93	0.010	4.34	0.057	3.74	0.075	1,11	0.09	0.776	1.03	0.333
Small-sized pollinators	1,13	20.46	< 0.001	20.46	< 0.001	13.36	0.003	11.47	0.005	1,11	0.65	0.436	1.52	0.243
Large-sized pollinators	1,13	16.24	0.001	16.24	0.001	4.97	0.044	1.86	0.195	1,11	0.00	0.991	1.37	0.266
All pollinators	1,13	16.22	0.001	16.22	0.001	14.99	0.002	10.02	0.007	1,11	0.46	0.513	1.79	0.208
Abundance														
All bees (Apoidea)	1,13	23.49	< 0.001	12.87	0.003	11.85	0.004	9.53	0.009	1,11	11.39	0.006	0.03	0.864
Solitary bees	1,13	11.37	0.005	2.42	0.142	6.54	0.024	12.52	0.004	1,11	8.95	0.012	0.00	0.985
Hoverflies (Syrphidae)	1,13	9.45	0.008	10.93	0.005	7.28	0.018	7.93	0.015	1,11	0.14	0.715	0.81	0.387
Small-sized pollinators	1,13	29.06	< 0.001	23.77	< 0.001	16.65	0.001	19.01	0.001	1,11	0.49	0.449	1.34	0.271
Large-sized pollinators	1,13	21.48	< 0.001	11.81	0.004	1.76	0.208	0.89	0.435	1,11	0.18	0.896	1.16	0.304
All pollinators	1,13	27.43	< 0.001	23.76	< 0.001	16.91	0.001	15.78	0.002	1,11	0.53	0.484	1.39	0.263

The rate of pre-dispersal fruit predation of *R. sativus* was significantly higher in ECA (28%) than in intensively managed meadows (21%; $F_{1,35} = 5.65$, $P = 0.023$).

Discussion

FLOWER-VISITING INSECTS

Our results demonstrate that ECA can serve as source areas for pollinating insects in the Swiss agricultural landscape. First, apart from butterflies, species richness and abundance of all pollinator guilds on flowers of three phytometer species were markedly enhanced in

Table 4. Summary of nested ANOVAS testing the effect of management (contrast: ECA vs. IM) and distance (contrast: log-distance from ECA within IM) on measures of reproductive success of *R. sativus*, *C. glomerata* and *H. radicata* at the level of the pot station. Fruit set, proportion of flowers that developed into fruits. Significant statistics shown in bold.

		Management		Distance	
Parameters of reproductive success	d.f.	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Raphanus sativus</i>					
Fruit set (%)	1,32	5.13	0.031	3.10	0.088
Number of seeds per fruit	1,35	0.43	0.515	0.02	0.894
Number of seeds per plant	1,32	6.90	0.013	3.69	0.064
Seed mass per fruit (g)	1,33	3.00	0.078	2.55	0.119
<i>Campanula glomerata</i>					
Number of seeds per fruit	1,28	4.36	0.046	1.33	0.258
Number of seeds per plant	1,19	4.65	0.044	2.00	0.174
Seed mass per fruit (g)	1,21	3.82	0.064	0.63	0.438
<i>Hypochaeris radicata</i>					
Number of seeds per fruit	1,28	2.18	0.151	0.15	0.700
Seed mass per fruit (g)	1,28	1.01	0.324	3.52	0.071

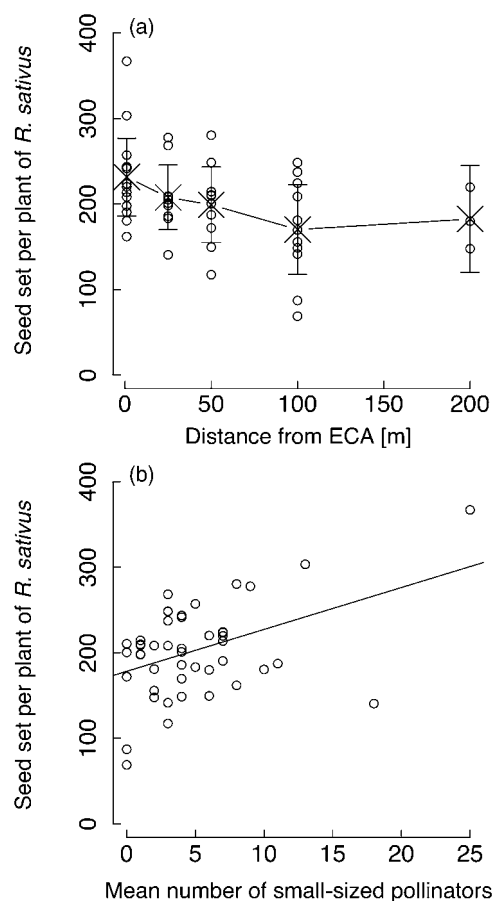


Fig. 2. (a) Number of seeds per plant of *R. sativus* (mean \pm 1 SE) in ECA (0 m) and at distances of 25 m, 50 m, 100 m ($n = 13$) and 200 m ($n = 4$) from the ECA within the IM. (b) Relationship between the number of seeds per plant of *R. sativus* and the number of small-sized pollinators per 60-min sample time. Untransformed data are shown.

Table 5. Summary of simple linear regression analyses testing the effects of species richness and abundance of pollinator groups per 60 min of sample time on measures of reproductive success of *R. sativus* and *C. glomerata* at the level of the station. No significant relationship was found between either abundance or species richness of pollinators and any measure of reproductive success in *H. radicata* (results not shown). Fruit set, proportion of flowers that developed into fruits; seed set fruit, number of seeds per fruit; seed set plant, number of seeds per plant; small-sized pollinators, mainly flies (except two large hoverfly species) and solitary bees; large-sized pollinators, bumblebees, honeybees, butterflies and two large hoverfly species (see the Materials and methods). Significant statistics shown in bold.

Pollinator group	<i>Raphanus sativus</i>									<i>Campanula glomerata</i>								
	Fruit set			Seed set plant			Seed mass			Seed set plant			Seed mass					
	<i>n</i>	<i>R</i> ²	<i>P</i>	<i>R</i> ²	<i>P</i>		<i>n</i>	<i>R</i> ²	<i>P</i>	<i>n</i>	<i>R</i> ²	<i>P</i>	<i>n</i>	<i>R</i> ²	<i>P</i>			
Species richness																		
All bees (Apoidea)	45	0.127	0.014	0.093	0.037		49	0.159	0.004	34	0.270	0.001	35	0.009	0.586			
Solitary bees	45	0.170	0.004	0.108	0.024		49	0.143	0.006	34	0.117	0.041	35	0.001	0.854			
Hoverflies (Syrphidae)	45	0.007	0.570	0.038	0.188		49	0.045	0.137	34	0.008	0.595	35	0.047	0.200			
Small-sized pollinators	45	0.114	0.020	0.102	0.029		49	0.080	0.045	34	0.015	0.484	35	0.050	0.183			
Large-sized pollinators	45	0.000	0.980	0.000	0.973		49	0.039	0.164	34	0.194	0.007	35	0.009	0.577			
All pollinators	45	0.092	0.039	0.089	0.042		49	0.087	0.035	34	0.089	0.077	35	0.042	0.224			
Abundance																		
All bees (Apoidea)	45	0.179	0.003	0.121	0.016		49	0.188	0.002	34	0.189	0.008	35	0.043	0.219			
Solitary bees	45	0.216	0.001	0.133	0.012		49	0.170	0.003	34	0.117	0.041	35	0.001	0.854			
Hoverflies (Syrphidae)	45	0.026	0.277	0.099	0.032		49	0.059	0.086	34	0.021	0.395	35	0.060	0.144			
Small-sized pollinators	45	0.227	0.001	0.202	0.002		49	0.135	0.008	34	0.045	0.215	35	0.089	0.073			
Large-sized pollinators	45	0.000	0.947	0.000	0.997		49	0.045	0.134	34	0.100	0.061	35	0.047	0.197			
All pollinators	45	0.194	0.002	0.194	0.002		49	0.157	0.004	34	0.089	0.077	35	0.105	0.051			

ECA compared with IM. Secondly, small-sized pollinators in IM declined with increasing distance from ECA, whereas no significant decline was found for pollinators of large body sizes.

Using a pairwise comparison of ECA with intensively managed meadows, Knop *et al.* (2006) found significantly more species of wild bees in ECA. Similarly, an evaluation of the Dutch agri-environment scheme demonstrated enhanced species richness of hoverflies and bees in grasslands where the first seasonal agricultural activities were delayed compared with conventionally managed meadows (Kleijn *et al.* 2001). The diversity of flower-visiting bees to cereal fields was enhanced in organic compared with conventionally managed fields in Germany (Holzschuh *et al.* 2007). Our analyses suggest that the observed increases in species richness and abundance of pollinator guilds in ECA is primarily governed by increases in plant species richness and flower abundance. For solitary bees and bumblebees better nesting opportunities (Potts *et al.* 2003), and for hoverflies more diverse larval food resources (Lagerlof & Wallin 1993), may have contributed to the observed increases in abundance and diversity in these pollinator taxa in ECA compared with IM. In our study, the age of ECA had a significant positive influence on species richness and abundance of bees, which indicates that the positive effects of the scheme are likely to increase with longer term extensification (Herzog *et al.* 2005).

Several studies have reported a positive correlation between habitat size and the abundance and diversity of insect pollinators (Aizen & Feinsinger 1994; Lennartsson 2002) but the present study and others (Gathmann,

Greiler & Tschardtke 1994; Donaldson *et al.* 2002) have not. Therefore, we conclude that, in the highly patterned Swiss agricultural landscape, the quality of an ECA is more important for a diverse pollinator assemblage than its size. This is in accordance with other studies demonstrating that even small habitat fragments of less than 1 ha can support a diverse pollinator community if sufficiently high densities of flowering plants occur (Kemper, Cowling & Richardson 1999; Donaldson *et al.* 2002).

The significant exponential decline of species richness and abundance of small- but not of large-sized pollinator guilds with increasing distance from ECA indicates that body size is a key trait of pollinators for movement from ECA into IM. We believe that this finding is of general importance for understanding pollinator movements in fragmented habitats (Steffan-Dewenter & Tschardtke 1999; Gathmann & Tschardtke 2002). However, body size corresponded to some degree with taxonomic differences between pollinator groups in our study: large-sized pollinators were mainly bumblebees *A. mellifera* and butterflies and only two species of large hoverflies; small-sized pollinators were essentially solitary bees and flies.

Despite the ability of hoverflies to disperse over long distances (Schneider 1948), our results suggest rather restricted average foraging movements of anthophilous hoverflies, with most foraging occurring within approximately 100 m of ECA. This fits well with measured dispersal distances of three hoverfly species from field margins into adjacent crops, with an exponential decline within approximately 100 m and little further decline thereafter (Wratten *et al.* 2003). Our findings also indicate that the average foraging range of solitary bees

inhabiting ECA is largely restricted to the ECA itself and to directly adjacent IM. Maximum foraging ranges of solitary bees are limited (Gathmann & Tscharntke 2002) and the average foraging ranges of solitary bees normally differ markedly from their maximum flight ranges (Ghazoul 2005). In agreement with our study, bees in coffee farms in Costa Rica (Ricketts *et al.* 2004) and solitary bees in grapefruit plantations (Chacoff & Aizen 2006) declined significantly within 100 m of nearby forest remnants. In the German agricultural landscape, solitary bees responded most strongly to the proportion of semi-natural habitats at the smallest, most local, spatial scale (radius 250 m), whereas social bees showed the strongest correlations at larger spatial scales (Steffan-Dewenter *et al.* 2002). Social bees were found to decline along isolation gradients from bee habitats for up to several hundred metres (Steffan-Dewenter & Tscharntke 1999; Kremen, Williams & Thorp 2002; Klein, Steffan-Dewenter & Tscharntke 2003a; Chacoff & Aizen 2006).

PLANT REPRODUCTIVE SUCCESS

A central question is whether the increased pollinator richness and abundance in ECA and their movement to adjacent IM leads to increased pollination and plant reproduction and thus further agricultural and conservation benefits. In the present study we found an increased overall production of seeds in ECA for two out of three phytometer species. However, as our experiment was limited to 1 year, the life-time reproductive success of the two perennial species *C. glomerata* and *H. radicata* could not be assessed.

Measures of the reproductive success of *R. sativus* and *C. glomerata* were positively correlated with species richness and abundance of pollinator guilds, which indicates that the increased reproductive success in these two plant species in ECA compared with IM resulted from reduced pollen limitation. In *R. sativus*, increased reproduction was mainly the result of increased seed number, and in *C. glomerata* with increased seed mass. These findings demonstrate that different plant species can adjust total reproductive effort to changing pollinator abundance and diversity in different ways (Schmid 1992). The reproductive success of *H. radicata* appeared not to be limited by pollinator richness and abundance. Indeed, we captured twice as many pollinators on *H. radicata* than on the other two phytometer species. In other studies, increased reproductive success was correlated with higher resource availability (Dejong & Klinkhamer 1989). However, because we used the same soil in all pots, differential resource limitation should not be the reason for the observed results. Furthermore, plant patch size, density and purity (Kunin 1997; reviewed in Ghazoul 2005) and the size of the floral display (Ohashi & Yahara 1999) can indirectly affect reproductive success via altered foraging behaviour of pollinators (Kunin 1997; Ghazoul 2005). In our study, we followed Steffan-Dewenter & Tscharntke (1999) and used identical arrays of potted plants to rule out such confounding factors.

Because differential herbivory between ECA and adjacent grassland could still have affected plant reproductive success (reviewed in Crawley 1989; Cunningham 2000), we also measured the rate of pre-dispersal seed predation. A significantly higher proportion of fruits of *R. sativus* (28%) was attacked by herbivores in ECA than in IM (21%). Thus ECA management enhanced the two counteracting effects, pollination and fruit predation, on plant reproductive success. However, we cannot completely rule out the possibility that a small percentage of the larvae we found in fruits of *R. sativus* were larvae of natural enemies of fruit herbivores. In any case, the benefits from the increased visitation rates of all pollinator taxa except butterflies appeared to outweigh the negative effects of increased fruit predation, as the overall reproductive success of *R. sativus* (number of healthy seeds per plant) was significantly higher in ECA than IM.

For *R. sativus*, we detected a decline in the number of fruits and seeds per plant with increasing distance from ECA. Steffan-Dewenter & Tscharntke (1999) also found that the seed set of two self-incompatible plant species, *Raphanus sativus* and *Sinapis arvensis*, decreased along a distance gradient up to some hundreds of metres from semi-natural grassland, with the most pronounced reductions occurring within a distance of approximately 100 m from the habitat fragment. In another study, fruit set of *Coffea canephora* was negatively affected by distance from continuous natural forest for up to approximately 400 m (Klein, Steffan-Dewenter & Tscharntke 2003a).

DIVERSITY—ECOSYSTEM SERVICE RELATIONSHIPS

Although we could not measure the efficiency of pollinators directly, the results of the linear regression analyses for relationships between pollinator guilds and plant reproductive success suggested that bees were the most efficient pollinator guild in our study, exhibiting a high functional importance (Larsen, Williams & Kremen 2005). However, we could not disentangle the closely correlated effects of bee abundance and bee richness on the reproductive success of the phytometers. Generally, in studies of natural communities, it is impossible to separate strictly the effects of species richness and abundance, even though in a study by Klein, Steffan-Dewenter & Tscharntke (2003b) only bee diversity and not abundance significantly affected fruit set of *Coffea arabica*. In our study, both species richness and abundance of all pollinator guilds were increased in ECA, which was in turn related to greater plant diversity in ECA than in adjacent intensively used grassland. Thus it is conceivable that a stabilizing feedback loop exists between plant diversity → pollinator abundance/richness → plant reproduction → plant diversity. The differential responses of the phytometer species to the different ECA-enhanced pollinator guilds indicate a considerable level of redundancy in the investigated pollination systems (Memmott, Waser & Price 2004).

Long-distance foragers such as bumblebees, honeybees and butterflies generally showed relatively low abundances and, at least for *R. sativus*, seemed to be of minor importance. Thus long-distance foragers (usually expected to compensate for shortages in pollination services in fragmented, intensively managed agricultural landscapes) cannot guarantee sufficient pollination of all plant species (Steffan-Dewenter & Tschardt 1999; Steffan-Dewenter *et al.* 2002). In particular, rare and specialized plants may be affected negatively, as most generalist pollinators forage in a frequency-dependent manner that results in a greater constancy and fidelity to common species (reviewed in Chittka, Thomson & Waser 1999). This further emphasizes the crucial role of ECA and other semi-natural habitats as sources of diverse pollinator communities in intensively managed agricultural landscapes. In addition, ECA may provide some insurance against disruptions of plant–pollinator interactions in highly variable agroecosystems (Yachi & Loreau 1999; Kremen, Williams & Thorp 2002).

We conclude that ECA with minimum botanical quality standards effectively enhance both pollinator species richness and pollination services. According to our data and analyses, the quality of an ECA with respect to plant species richness is more important for a diverse pollinator community than its size. Therefore, the focus on achieving minimum botanical quality standards, as recently implemented in a by-law on ecological quality in Switzerland, is supported by our study. ECA with high plant diversities are sources of rich pollinator communities, which provide pollinator services within ECA and to surrounding intensively managed agricultural grassland. Our study also shows that these effects on pollinator services can be specific to particular pollinator guilds and pollinated plant species. We believe that these specificities do not reduce the general relevance of our findings for the implementation of ECA: the observed pronounced declines of small-sized pollinators emphasize the crucial role of sufficient connectivity of ECA and possibly other semi-natural habitats to maintain both diverse pollinator communities and sufficient pollination services to wild plant species and economically important crops in intensively managed agricultural landscapes. Farmers should be encouraged to participate in regional projects that aim to enhance connectivity between ECA and semi-natural habitats.

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