Running head: Enhancing arthropod diversity on grassland

Effects of ecological compensation meadows on arthropod diversity in adjacent intensively managed grassland

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Abstract

An important goal of ecological compensation areas (ECAs) is to increase biodiversity in adjacent intensively managed farmland and the agricultural landscape at large. We tested whether this goal can be achieved in the case of the agri-environmental restoration scheme implemented for Swiss grassland using five large arthropod taxa (bees, true bugs, orthopterans, ground beetles and spiders) representing different ecological and functional groups. The species richness and abundance of all groups and species, respectively, was measured along 100 m transects from ECA-meadows into the adjacent intensively managed grassland at 24 sites. Species richness of all arthropod taxa except ground beetles, and the abundance of 63% of the 234 arthropod species sampled with at least five individuals were higher in ECA-meadows than in their surroundings, while the total abundance of spiders and ground beetles was higher in intensively managed meadows. The abundance of 8% of these species were only increased in the ECA-meadows themselves (“stenotopic” species) but 40% had increased abundance both in the ECA-meadows and the adjacent grassland, declining exponentially with increasing distance from ECA-meadows (“edge species”). The 90%-decay distances for these edge species differed among taxonomic groups (117 ± 18 m for true bugs, 137 ± 24 m for spiders, 152 ± 34 m for bees, 167 ± 5.7 m for orthopterans, 185 ± 34 m for ground beetles; mean ± 1 standard error) and independent of taxonomic group were larger for large-sized or predacious species than for small-sized or phytophagous species. Because the average distance between neighbouring ECA-meadows in Swiss grassland is only 73 ± 4 m, the current agri-environment scheme very likely enhances arthropod diversity and possibly associated ecosystem services in the Swiss agricultural landscape at large.

Key words

Agri-environment schemes, arthropod diversity, body size, meadow restoration, positive edge effect, trophic guild

1. Introduction

Agricultural intensification and the concomitant fragmentation of semi-natural habitats have been widely recognized as a serious threat to biodiversity (Robinson and Sutherland, 2002; Benton et al., 2002). Agri-environment schemes aim at counteracting the adverse effects of modern agriculture on biodiversity and at improving the general status of the environment by providing financial incentives to farmers for ecologically enhancing their land (OECD, 2003). Currently, these schemes cover approximately 25% of the farmed land of the 15 older member states of the European Union (Kleijn et al., 2006) and cost yearly around € 2.2 billion (OECD, 2003). Hence, agri-environment schemes are considered the most important policy instrument to preserve and restore biodiversity in European agricultural landscapes (Vickery et al., 2004; Kleijn et al., 2006). The most important measure of the Swiss agri-environment scheme is that at least 7% of the farmland must be managed as ecological compensation areas (ECAs). These include a wide range of specific biotopes such as wild-flower strips, orchards, hedges or extensively managed hay meadows. ECA-meadows constitute by far the most widespread ECA type in Switzerland, making up 87% of the total ECA-area in 2007 (BLW 2008). The management prescriptions for ECA meadows (hereafter abbreviated with ‘ECAs’) include postponed mowing and prohibition of fertilizer application.

The success of agri-environment schemes in conserving and restoring farmland biodiversity is difficult to assess because they are poorly monitored (Kleijn

and Sutherland, 2003). Some schemes have found to deliver mixed biodiversity benefits (Kleijn and Sutherland, 2003; Kleijn et al., 2006), whereas others, such as the Swiss scheme, have been more effective in preserving biodiversity (Albrecht et al., 2007a). The presence of target species, effective prescriptions, and the size and spatial arrangement of areas under agri-environment schemes are crucial to produce benefits to biodiversity (Ovenden et al., 1998; Vickery et al., 2004; Kleijn et al., 2006; Pywell et al., 2006).

An important missing link in the assessment of the effectiveness of the mentioned schemes is how ECAs affect biodiversity in the surrounding intensively managed farmland. The distribution and abundance of populations and their biotic interactions often depend on processes that are not confined to local habitat patches (e.g. Tscharntke et al., 2005). The resource use of species in agroecosystems is not restricted to a single habitat, but most species depend on complementary habitat resources to successfully complete their life cycle (Duelli and Obrist, 2003; Tscharntke et al., 2005). Such movement and exchange between habitat patches may play a central role in shaping diversity patterns and community structure in the mosaic of areas under agri-environment schemes and the surrounding intensively managed farmland. These processes may have important implications for ecosystem functioning and services, for example by enhancing natural pest control (Altieri, 1994) or pollination (Kremen et al., 2002; Albrecht et al., 2007a). Moreover, ecological resilience and the sustainability of agroecosystems may depend on a broad spectrum of biodiversity including a high diversity of functional groups (Bengtsson et al., 2003; Balvanera et al., 2006).

The aim of this study is fourfold. First, we examine whether restored meadows managed according to the prescriptions of the Swiss agri-environment scheme (ECA-

meadows) sustain more species and individuals of different functional groups of arthropods and plants than intensively managed grasslands. Second, we quantify the proportion of arthropod species exhibiting positive edge effects along gradients from restored into surrounding intensively managed grassland. Third, we estimate 90%-decay distances radiating out from ECA-meadows for the investigated species groups and compare them with average distances between ECA-meadows in the Swiss agricultural landscape. Finally, we analyse the influence of body size and trophic level on these decay distances.

We measured species richness and abundance of plants and of five groups of arthropods, i.e. bees (Hymenoptera: Apoidea), true bugs (Heteroptera), orthopterans (Orthoptera), ground beetles (Coleoptera: Carabidae) and spiders (Araneae) along gradients from 24 ECA-meadows into adjacent intensively managed grassland. Ground beetles, spiders and predacious bugs are important bio-control agents (Fauvel, 1999; Symondson et al., 2002) and bees represent the most important pollinator group in agroecosystems (Kremen et al., 2002). Thus, it can be expected that, by increasing their biodiversity, ecosystem services provided by the groups can also be enhanced.

2. Material and methods

2.1. Study design and sampling protocol

Bees, true bugs, orthopterans, ground beetles and spiders were sampled on 24 sites (18 in 2003 and 6 additional ones in 2004) from ECA-meadows and from adjacent intensively managed grassland. These sites were located in the Cantons of Zurich, Aargau, Lucerne and Basel Land and represented the typical agricultural landscape of the Swiss lowlands, consisting of a small-scale mosaic of grasslands, arable fields and forests. The sites were not or only slightly sloped and ranged from 385 to 710 m

126 above sea level. The average minimal distance between sites was 3.2 ± 0.7 km,
127 ranging from 1.2 to 13.7 km. The selected ECA-meadows were identical to the
128 adjacent intensively managed grasslands in exposition and slope and had been under
129 the agri-environment scheme for at least 5 years. The average size of an ECA-
130 meadow was 0.86 ± 0.13 ha, ranging from 0.20 to 2.83 ha. The average
131 perimeter/area ratio of an ECA-meadow was 0.071 ± 0.006 (range: 0.028 – 0.118).
132 No significant effect of ECA-meadow size or perimeter/area ratio on species richness
133 or abundance of arthropods was found (all $P > 0.05$). In the year of the arthropod
134 sampling the selected ECA-meadows were cut 1.9 ± 0.1 times, whereas intensively
135 managed meadows were cut 4.2 ± 0.2 times. As prescribed by the Swiss agri-
136 environment scheme, all ECA-meadows were cut the first time after 15 June. The first
137 cut of the intensively managed meadows took mostly place in the first half of May. A
138 further ECA-meadow management prescription was that the application of any
139 fertilizer was prohibited. On the other hand, all intensively managed meadows were
140 fertilized by liquid manure. To avoid possible confounding effects from semi-natural
141 habitats, only sites without such structures within approximately 100 m were chosen.
142 Since semi-natural landscape elements could also have affected arthropod
143 communities in focal meadows at an even larger spatial scale, the percentage semi-
144 natural habitat was recorded within a perimeter with a radius of 750 m and its
145 influence tested on species richness and abundance of spiders, true bugs and
146 orthopterans. The average proportion of semi-natural habitat and the variation in this
147 proportion was low ($3.9 \pm 0.4\%$, ranging from 1.6 to 7.9%). No significant effect of
148 the percentage semi-natural habitat on the species richness and abundance of the three
149 arthropod taxa was detected (all $P > 0.05$; Grimm, 2005).

Spiders and ground beetles were captured with pitfall traps (funnel traps; upper diameter of the funnel: 15 cm). This trap type is recommended due to its very high trapping efficiency (Obrist and Duelli, 1996). At each site, always one funnel trap was located in the ECA-meadow (at 10 m distance from the borderline between the ECA-meadow and the adjacent intensively managed grassland) and at distances of 25, 50 and 100 m from the ECA-meadow in the adjacent intensively managed grassland. In both years, the traps were emptied bi-weekly between the last week of April and the last week of September. Pitfall traps measure activity-density of ground-dwelling arthropods. For simplicity, here we use the term “abundance” when referring to the number of individuals, irrespective of the sampling method.

Wild bees were sampled by transect surveys with a bioquip 7112NA student net (diameter 40 cm; BioQuip Products, Rancho Dominguez, CA). During 15 minutes each bee that was observed on a 1-m wide transect parallel to the borderline between the ECA-meadow and the adjacent intensively managed grassland was captured (Banaszak, 1980; Kleijn et al., 2006; Knop et al., 2006). Bee transect surveys were made at the same distances from the borderline between ECA-meadow and intensively managed grassland as the pitfall samplings. Further arthropods, especially orthopterans and true bugs, were sampled by using the same transect as for the bees but sweeping a bioquip 7625HS heavy duty net 60 times over the ground within each transect (general sweep netting). Sampling with these two methods was not done at the same date to avoid interference among them. In both years, three survey rounds were carried out with the bee transect and four with the general sweep netting method. These surveys were done between May and September, on sunny days from 10 am to 4 pm. The sampled bees, orthopterans, bugs and spiders were sorted out for further analysis.

The cover of individual plant species and the total number of plant species were recorded from May–June in both years within five plots of 2 x 5 m, arranged on both sides of each pitfall trap at an interval of 2.5 m and parallel to the borderline between ECA-meadow and intensively managed grassland.

2.2. *Classification of arthropods*

Each arthropod specimen was identified to species level. Each species was assigned to ecological groups according to body size and trophic level. Species were classified into the four size classes “large”, “medium”, “small” and “very small” and the three trophic guilds “predators”, “herbivores” and “omnivores”. The classification of Apoidea, Araneae, Carabidae and Heteroptera is based on Schweiger et al. (2005). Body size and trophic level of species not assigned in Schweiger et al. (2005) were obtained from the literature (the authors will provide references on request).

2.3. *Data analysis*

To analyse variation in abundance and species richness of arthropod groups (both ecological and taxonomic groups) and species richness of plants, we fitted general linear models with site as blocking factor and distance as treatment factor (ECA-meadow, 25, 50 and 100 m). The distance factor was decomposed into a management contrast (ECA-meadow vs. intensively managed grassland), a log-distance contrast (increasing distance within intensively managed grassland) and the remaining deviation from log-linearity (within intensively managed grassland). We used a log-distance contrast in all analyses, because it fitted the data better than a linear distance contrast (see Results section). The general linear model was fitted for each taxon, trophic level and size class separately using the pooled data of all survey rounds over

both seasons. The covariate “plant species richness” was entered before the distance contrast into the statistical model.

In order to quantify the proportion of arthropod species in ECA-meadows and surrounding intensively managed grasslands contributing to a positive edge effect of ECA-meadows into adjacent intensively managed grasslands the following procedure was applied: first, we excluded all species with less than five recorded specimens from the dataset (45% of the total number of arthropod species). For each of the remaining 234 species we fitted negative exponential functions ($y = e^{a-b\sqrt{D}}$, where a and b are parameters and D is the distance from ECA-meadow) to the combined number of captured individuals of all sites. The exponential function fitted the data better than exponential power and Weibull functions (data not shown). To eliminate between-site variation, we normalized captures among sites (e.g. Cronin et al., 2000). We used PROC NLIN procedure provided by the SAS statistical software package (version 8.2, SAS Institute Inc., Cary, North Carolina) to estimate the parameters of the function.

Each species was assigned to one of the three distribution types “stenotopic” species, “edge” species or “other” species according to its distribution pattern along the sampled gradient (Duelli and Obrist, 2003). Species only occurring in the ECA-meadow were classified as stenotopic species for ECAs. A few species occurred with at least 20 individuals in the ECA-meadows and negligible abundance in the intensively managed grasslands (≥ 20 times lower abundance in intensively managed grasslands than in ECA-meadows). These species were also attributed to the distribution type “stenotopic species”. Of the remaining species, those exhibiting a significant fit to the negative exponential function ($P \leq 0.05$) were classified as edge species. The remaining species were classified as other species (i.e. “ubiquistic”

species occurring at similar densities in the two habitat types and species occurring at higher densities in intensively managed habitat; since we were mainly interested in the effects of ECA-meadows as source habitats supplying nearby intensively managed grassland habitat and for the sake of simplicity we did not separate the latter two species groups).

The spatial extent of abundance and diversity gradients radiating out from ECA-meadows into intensively managed grasslands is difficult to measure accurately due to the exponential nature of such effects (e.g. Hylander, 2005). Following Hylander (2005), 90%-decay distances were estimated as the distance where the abundance declined to 10% of that found in the ECA-meadow. Decay distances were only estimated for edge species. A general linear model was used to analyse the effects of taxon, trophic level and body size on 90%-decay distances. As only two edge species were omnivorous, only herbivores and predators were included in this analysis.

Log-linear models and analysis of deviance were used to explore the effects of trophic guild and body size on the distribution type of species (Crawley, 2005). Distribution type was decomposed into the contrasts edge species vs. rest (contrast 1) and stenotopic species vs. other species within rest (contrast 2). To test the relationship between these contrasts and body size or trophic level we fitted the interaction between the contrasts and the trait factors.

To compare the 90%-decay distances of different arthropod groups with the average minimum distance between ECA-meadows in the Swiss lowland agricultural landscape, the distance between 522 ECA-meadows and their nearest neighbouring ECA-meadow was calculated. A total of 56 municipalities distributed all over the Swiss lowlands were selected by a stratified random sampling (see Herzog et al.,

2005). The ECA-meadows were mapped during the years 1999 and 2000, digitised and analysed by means of a geographical information system (subsequent versions of ArcInfo). For the analysis of average ECA-meadow distances, those within a 200 m buffer of the municipalities' borders were excluded, thus avoiding possible bias introduced by ECA-meadows located peripherally at municipality boundaries. This restriction reduced the number of municipalities to 26. The mean distance between nearest neighbour ECA-meadows in the Swiss lowlands was 72.6 ± 4.0 m.

Except for the fitting of the decay functions, all statistical analyses were performed in R (R Development Core Team 2008). Abundances of all arthropod groups were square-root transformed to achieve normality and homoscedasticity (Crawley, 2005). Unless otherwise stated, arithmetic means ± 1 standard error are reported.

3. Results

3.1. Taxonomic groups

A total of 144,630 arthropod individuals belonging to 423 species were sampled. Of these, 234 species were represented by at least five specimens (Table 1). Total arthropod species richness and the abundance of 63% of the 234 arthropod species sampled with at least five individuals were higher in ECA-meadows than in adjacent intensively managed grasslands (Table 2, Fig. 1). Similarly, species richness and abundance of true bugs, bees and orthopterans and species richness of spiders was higher in restored than in intensively managed grasslands (Table 2, Fig. 1). In contrast, the abundance of the two taxa with most individuals sampled, spiders and ground beetles, and thus also total arthropod abundance, was higher in intensively managed grasslands than in ECA-meadows (Table 2, Fig. 1). Species richness and

abundance of bees and true bugs, species richness of ground beetles and total species richness of all arthropods declined with increasing distance from ECA-meadows (Table 2, Fig. 1). Of the species sampled with at least five specimens 8% were restricted to ECA-meadows (“stenotopic” species) whereas 40% were “edge” species, exponentially declining with increasing distance from ECA-meadows.

Plant species richness was significantly higher in ECA-meadows than in intensively managed grasslands ($F_{1,23} = 446.70$, $P < 0.001$), but did not decline with increasing distance from ECA-meadows ($F_{1,23} = 1.24$, $P = 0.278$) (Fig. 2). Plant species richness was positively related to the number of species and abundance of bees (ANCOVA: $F_{1,22} = 9.32$, $P = 0.006$; $F_{1,22} = 14.16$, $P = 0.001$) and the species richness of true bugs ($F_{1,22} = 4.98$, $P = 0.036$), but was negatively correlated with spider abundance ($F_{1,22} = 7.40$, $P = 0.013$).

3.2 Ecological groups

Species richness and abundance of phytophagous and omnivorous arthropods was higher in ECA-meadows than in intensively managed grasslands, while predator abundance showed the opposite pattern (Table 2, Fig. 3). Species richness of all three trophic guilds and the abundance of phytophagous arthropods declined with distance from ECA-meadows (Table 2, Fig. 3). Species richness of small-sized ($F_{1,23} = 99.51$, $P < 0.001$), medium-sized ($F_{1,23} = 160.57$, $P < 0.001$) and large-sized arthropods ($F_{1,23} = 101.35$, $P < 0.001$), and the abundance of very small ($F_{1,23} = 25.70$, $P < 0.001$) and small arthropods ($F_{1,23} = 58.50$, $P < 0.001$) was higher in ECA-meadows than in adjacent intensively managed grasslands. Furthermore, the species richness ($F_{1,23} = 20.83$, $P < 0.001$) and abundance ($F_{1,23} = 18.44$, $P < 0.001$) of small-sized and the species richness of medium-sized ($F_{1,23} = 19.31$, $P < 0.001$) and marginally

significantly also that of large-sized arthropods ($F_{1,23} = 3.08$, $P = 0.093$) decreased with increasing distance from ECA-meadows.

Edge species included more phytophagous and less predacious species than expected ($G^2 = 12.76$, $df=1$, $P \leq 0.001$) and were larger ($G^2 = 5.78$, $df=1$, $P = 0.017$) than stenotopic and other species (Table 1). Furthermore, stenotopic species included less predacious and more other species than expected ($G^2 = 12.68$, $df=1$, $P \leq 0.001$).

Both body size and trophic level significantly affected 90%-decay distances of species: large and predacious species showed larger decay distances than small and phytophagous species (Table 3,4). While the taxonomic identity *per se* had no significant effect on decay distance, the interaction of taxonomic group with body size was significant, indicating a taxon-specific effect of body size (Table 4).

4. Discussion

4.1. Increased plant and arthropod diversity in ECA-meadows

Grassland restoration according to the prescriptions of the Swiss agri-environment scheme significantly enhanced species richness of all arthropod taxa (except ground beetles) and plants. Sixtythree per cent of the 234 arthropod species sampled with at least five specimens occurred in higher densities in restored grassland than in adjacent intensively managed grassland. These percentages are probably conservative estimates, because due to the higher number of sampling points the probability of detecting a very rare species in intensively managed grasslands was higher than detecting such a species in ECA-meadows. Our findings corroborate recent research documenting enhanced species richness of plants, bees, hover flies and orthopterans in ECA-meadows compared with intensively managed grasslands in Switzerland (Herzog et al., 2005; Knop et al., 2006; Albrecht et al., 2007a, 2007b). Plant species

richness in agricultural meadows has been found to be negatively correlated with both intensity of fertilizer and mowing intensity (Zechmeister et al., 2003). A wide range of plant species cannot effectively use increased nitrogen inputs and are generally out-competed by the few species that can use increased nitrogen levels for increased biomass production, a process that has recently been suggested to be driven mainly by competition for light (Hautier et al., 2009). Early and frequent mowing strongly increases the competitive dominance of fast growing species and may prevent late flowering species from pollination and seed production (Jantunen et al., 2007). The higher arthropod species richness in ECA-meadows might be explained by a bottom-up effect of plant species richness on primary consumer diversity, which in turn may have facilitated the observed increase in spider species richness at the third trophic level (Siemann, 1998; Balvanera et al., 2006). The increased species richness and abundance of bees in ECA-meadows compared with intensively managed meadows was probably primarily a consequence of the higher and more continuous floral resource availability in ECA-meadows, i.e. an increased flower abundance and species richness of flowering plants (Pywell et al., 2006; Albrecht et al., 2007a). Better nesting opportunities for ground-nesting bees may also have played a role (Potts et al., 2005). Our results are in a line with those of studies on the effects of mowing regime on single arthropod taxa, suggesting that earlier and more frequent cutting of meadows affect true bug (Di Giulio et al., 2001), orthopteran (Guido and Gianelle, 2001) and spider diversity (Baines et al., 1998) more negatively than ground beetle diversity (Morris, 2000; Humbert et al., 2009). Hay harvesting can affect arthropods in at least three ways: i) direct mortality during the harvest process, ii) changes in the physical structure of the swards, which is associated with changes microclimatic conditions, iii) movements out of short cut swards due to a lack of resources and

increased predation risk or movements into mown fields (see 4.2) (Guido and Gianelle, 2001; Haysom et al., 2004; Humbert et al., 2009). As predicted by resource concentration hypothesis (Root, 1973) several studies have found higher abundances of arthropod taxa at higher fertilization levels of grasslands, as plant productivity increases, and as plant composition shifts to a few dominant plant species with high tissue quality (Strong et al., 1984; Siemann, 1998; Haddad et al., 2000). In a line with these studies, the abundance of the two taxa sampled with highest numbers of individuals, spiders and ground beetles, and thus also total abundance, was higher in the intensively managed grasslands than in the ECA-meadows, but not that of bees, true bugs or orthopterans. This suggests that also prey abundance of spiders and ground beetles, mostly generalist predators, was higher in intensively managed meadows. It is also conceivable that the vegetation structure of the intensively managed meadows is more favourable to cursorial movement of the ground dwelling spiders and ground beetles (Symondson et al., 2002). In contrast, the higher abundances of the generally more specialized true bugs and orthopterans in ECA-meadows are probably primarily a consequence of the increased plant diversity and the lower mowing frequency in these meadows.

4.2 Influence of ECA-meadows on surrounding intensively managed grasslands

We could detect positive edge effects from restored into adjacent intensively managed grassland in a large number of arthropod species (94 out of 234 species sampled with at least five specimens). The typical exponential decline with increasing distance from ECA-meadow was not due to a decline in plant diversity, which was constantly low across the intensively managed grasslands. This suggests that the management regime in these meadows was probably too intensive and competition with species well

adapted to such conditions too strong for a detectable?? successful colonization of new plant species from ECA-meadows. Increased abundance and diversity of arthropods in the proximity of these ECA-meadows may positively affect the level of ecosystem functions and services in intensively managed grasslands (Albrecht et al., 2007a).

We suggest that the following three potentially interrelated processes most likely caused the abundance and diversity gradients from restored into intensively managed grasslands: i) passive dispersal of arthropods reproducing or overwintering in ECA-meadows into intensively managed grasslands, ii) foraging from restored into intensively managed grasslands of arthropods reproducing or overwintering in ECA-meadows and iii) refuge seeking of arthropods foraging and reproducing mainly in intensively managed grassland into ECA-meadow habitat (Ries et al., 2004; Rand et al., 2006). Extensively managed meadows may generally be more favourable sites for reproduction and overwintering for grassland arthropods compared to intensively managed grasslands due to lower disturbance levels for reproduction and larval development and potentially better conditions for overwintering (Haysom et al., 2004). Nevertheless, intensively managed grasslands can provide ephemeral high quality resources for generalist arthropods (Symondson et al., 2002; Rand et al., 2006). Therefore, it is possible that many of the species identified as edge species, occurring at higher densities in ECA-meadows when looking at the entire season, have benefited from the transiently increased resource base provided by adjacent intensively managed grasslands (ii). However, it is also conceivable that transient concentration effects in ECA-meadows, caused by disturbances such as mowing or fertilizer application in intensively managed grasslands forcing surviving arthropods to search refuges in nearby ECA-meadows (iii), partly contributed to the observed

edge effects. Edge effects from intensively managed grassland into ECA-meadows were not investigated in this study, which is an interesting research area for future studies.

4.3. Decay distances of species radiating out from ECA-meadows into intensively managed grasslands

The spatial extent of edge effects is difficult to measure accurately, because of the exponential nature of most edge effects (e.g. Hylander, 2005). Because exponential functions never decay completely and are difficult to estimate at the tail (Kot et al., 1996), we used the distance at which the decay reached 90% (10% remaining) as a measure (Hylander, 2005). The estimated 90%-decay distances for most species were only slightly larger than the measured distance range from 0–100 m and can therefore be considered as minimal extrapolations.

Considering the dense network of ECA-meadows in the investigated landscapes of the Swiss lowlands dominated by grasslands, with an average distance of only 73 m between neighbouring ECA-meadows, these 90%-decay distances indicate that most of the surrounding matrix of intensively managed grasslands can be reached by the investigated arthropod species. Thus, our findings suggest that in regions where ECA-meadows are the prevailing type of ECAs the ECA-meadow-network may successfully increase arthropod diversity in the agricultural landscape at large.

4.4. Ecological groups

The large number of arthropod taxa investigated allowed us to analyse differences in edge effects among ecological groups of trophic guild and body size. We found

pronounced differences in the proportion of species showing edge effects among trophic guilds. About half of the investigated phytophagous species showed positive edge effects, whereas this proportion was approximately a third for predacious species. Predacious arthropods appeared to be much more ubiquitous, with about two thirds of all investigated species showing similar or even higher abundances in intensively managed grasslands compared to phytophagous species, of which a considerable percentage was stenotopic for ECA-meadows (14%) and less than 40% were ubiquitous. Among the edge species, phytophagous species had shorter 90%-decay distances than predacious species. These findings suggest that proximity to restored areas is an important factor shaping the community and trophic structure of the investigated grasslands. These ecological traits explained more variation in decay distances among species than did taxonomic traits. This supports suggestions of a recent study (Schweiger et al., 2005) that local arthropod communities in agricultural landscapes may primarily be structured by differences in body size and trophic guild. The observed positive relationship between body size and decay distance is predicted by allometric scaling laws (Peters, 1986; Woodward et al., 2005). However, a positive scaling holds only for active movement (Peters, 1986; Etienne and Olf, 2004). If movement is predominantly passive, very small species are expected to exhibit larger movement distances (Etienne and Olf, 2004). From the sampled arthropod taxa in our study, such passive dispersal by wind is known for very small, primarily linyphid spiders (“ballooning”) (Marc et al., 1999). Indeed, 90%-decay distances for species of this very small size guild were larger than for small size guilds of other arthropods.

5. Conclusions and implications

Studies on habitat fragmentation report edged effects on arthropod communities within habitat fragments (e.g. Laurance et al., 2002). In the context of ECAs, edge effects around ECAs may be desirable, because they can enhance arthropod diversity in surrounding habitat, as shown here for a large number of species covering a broad taxonomic and ecological spectrum. Our findings indicate that the different taxa and ecological groups differ considerably in the proportion of species and the spatial extent to which they show edge effects. From a conservation biological point of view, the enhanced species richness and abundance of arthropods in ECA-meadows and their surroundings is not only valuable in itself but has also the potential to promote ecosystem functions and services such as pollination and pest control in the intensively managed adjacent grassland and in the agricultural landscape at large, because distances between ECA-meadows in Switzerland are short. Our results have general implications for the planning of the spatial configuration of restored and protected areas in intensively managed landscapes, emphasizing that biodiversity and potentially associated ecosystem services are not confined to such habitats, but emanate to various extents into the surrounding intensively managed habitat, contingent on the ecological traits of a species. Our findings underline the critical role of a well connected network of ECAs in promoting biodiversity in the agricultural landscape at large. We recommend that farmers should be encouraged to participate in schemes that aim to enhance connectivity between ECAs.

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Table 1. Numbers of arthropod species and individuals sampled in ECA-meadows and at distances of 25, 50 and 100 m from the ECA-meadows within adjacent intensively managed grasslands (n = 24). Species sampled with at least five specimens were assigned to three distribution types according to their spatial patterning along the transects: stenotopic species for ECA-meadows, edge species exponentially declining with increasing distance from ECA-meadows and other species

Group	Number of		Number of species		Distribution type		
	Total	Nind ³ 5	Total	Nind ³ 5	Stenotopic species (%)	Edge species (%)	Other species (%)
Taxonomic							
Araneae	58.066	57.944	144	68	4	38	58
Gnaphosidae	348	345	9	6	0	100	0
Linyphiidae	15.929	15.892	46	23	9	13	78
Lycosidae	36.647	36.643	20	18	0	39	61
Theridiidae	186	173	10	4	0	25	75
Thomisidae	569	560	13	5	0	80	20
Other families	4.387	4.331					
Coleoptera (Carabidae)	54.011	53.955	102	70	1	30	69
Heteroptera	13.058	12.989	94	57	14	49	26
Anthracoridae	306	302	7	4	0	0	100
Lygaeidae	372	350	17	7	43	29	29
Miridae	9.944	9.926	31	22	14	55	32
Pentatomidae	575	567	12	7	14	86	0
Tingidae	823	823	5	5	60	40	0
Other families	1.038	1.021					
Hymenoptera (Apoidea)	4272	4194	69	28	0	50	50
Orthoptera	15.223	15.219	14	11	9	46	46
Acrididae	14.293	15.293	7	7	14	43	43
Other families	930	926					
Trophic							
Phytophagous	36.123	35.976	181	104	14	49	38
Predacious	105.531	105.357	229	123	3	33	63
Omnivorous	2.976	2.968	13	7	14	29	57
Body size							
Large	8.677	8.627	57	32	9	47	44
Medium	53.412	53.348	99	59	5	61	34
Small	24.359	24.241	120	65	11	35	54
Very small	58.182	58.085	147	78	8	26	67
Total	144.63	144.301	423	234	8	40	52

Table 2. Summary of ANOVAs testing the effects of management and distance from ECA-meadow on species richness and abundance of five arthropod taxa (pooled data of 24 transects). Management was tested as a contrast ECA-meadow vs. intensively managed grassland, and distance from ECA-meadow as a contrast log-distance from ECA-meadow within intensively managed grassland. Abundances of all arthropod taxa were square-root transformed. Values in italics indicate effects in opposite direction to the hypothesis, i.e. ECA-meadows < intensively managed grasslands.

Arthropod taxa	Df	Management		Log-distance	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Number of species					
Spiders	1,23	39.76	< 0.001	0.71	0.408
Ground beetles	1,23	0.49	0.492	6.84	0.015
True bugs	1,23	309.33	< 0.001	14.3	0.001
Bees	1,23	103.58	< 0.001	8.42	0.008
Orthopterans	1,23	10.92	0.003	2.25	0.158
Phytophagous	1,23	454.37	< 0.001	28.59	< 0.001
Predacious	1,23	0.01	0.921	6.55	0.018
Omnivorous	1,23	5.01	0.035	19.22	< 0.001
Total	1,23	150.26	< 0.001	16.13	0.001
Number of individuals					
Spiders	1,23	<i>13.54</i>	0.001	0.06	0.815
Ground beetles	1,23	22.35	< 0.001	0.87	0.361
True bugs	1,23	211.99	< 0.001	21.02	< 0.001
Bees	1,23	112.5	< 0.001	13.38	0.001
Orthopterans	1,23	74.38	< 0.001	0.15	0.707
Phytophagous	1,23	271.61	< 0.001	13.03	0.002
Predacious	1,23	<i>46.84</i>	< 0.001	0.27	0.609
Omnivorous	1,23	26.54	< 0.001	0.1	0.754
Total	1,23	<i>7.32</i>	0.013	0.01	0.922

Table 3. Estimation of the 90%-decay distance (mean $\pm$ 1 standard error) radiating out from ECA-meadows into intensively managed grasslands for five arthropod taxa, two trophic guilds and four size classes. For the calculation of the 90%-decay distance see Methods section. Included are only species with a significant ($P \leq 0.05$) decline with distance from ECA-meadows into intensively managed grasslands, i.e. species classified as edge species.

Group	90%-decay distance
Taxonomic	
Araneae	137 ($\pm$ 24)
Carabidae	185 ($\pm$ 34)
Heteroptera	117 ($\pm$ 18)
Apoidea	152 ($\pm$ 34)
Orthoptera	167 ($\pm$ 57)
Trophic	
Phytophagous	125 ($\pm$ 15)
Predacious	171 ($\pm$ 22)
Body size	
Large	176 ($\pm$ 39)
Medium	145 ($\pm$ 21)
Small	130 ($\pm$ 22)
Very small	141 ($\pm$ 25)

Table 4. Results of ANOVA testing the effects of taxonomic status, trophic position and body size on 90%-decay distances radiating out from ECA-meadows into intensively managed grasslands. The five taxonomic groups are bees, true bugs, orthopterans, ground beetles and spiders. The two trophic guilds are herbivores and predators. For the calculation of the 90%-decay distance see Methods section. Included are only species with a significant ($P \leq 0.05$) decline with distance from ECA-meadows into intensively managed grasslands, i.e. species classified as “edge species”.

Source	Df	<i>F</i>	<i>P</i>
Taxonomic group	4	1.42	0.235
Trophic guild	1	8.27	0.005
Body size	1	5.09	0.027
Taxonomic group x trophic guild	1	3.16	0.079
Taxonomic group x body size	4	2.82	0.031
Trophic guild x body size	1	0	0.985
Taxonomic group x trophic guild x body size	1	0.06	0.81
Error	75		

Figure legends

Fig. 1. Mean number (± 1 standard error) of (a) individuals and (b) species of bees, true bugs, orthopterans, ground beetles, spiders and all arthropod taxa combined in ECA-meadows (0 m) and at distances of 25, 50 and 100 m from the ECA-meadows within intensively managed grasslands. For better visualisation, abundance of Apoidea was multiplied by five at each distance. Untransformed, pooled data of 24 transects are shown.

Fig. 2. Mean number (± 1 standard error) of vascular plant species in ECA-meadows (0 m) and at distances of 25, 50 and 100 m from the ECA-meadows within intensively managed grasslands. Untransformed, pooled data from five 2 x 5 m plots at each distance class of 24 transects are shown.

Fig. 3. Mean number (± 1 standard error) of (a) individuals and (b) species of predators, pollinators and herbivores in ECA-meadows (0 m) and at distances of 25, 50 and 100 m from the ECA-meadows within intensively managed grasslands. For better visualisation, pollinator abundance was multiplied by 50 and pollinator species richness by five at each distance. Untransformed, pooled data of 24 transects are shown.

Fig. 1

Fig. 2

Fig. 3