Response of ground beetle (Coleoptera, Carabidae) communities to changes in agricultural policies in Sweden over two decades

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ABSTRACT

Agricultural intensification has been recognized as an important driver of declines in biodiversity and ecosystem services. Changes in agricultural policy aims to mitigate these declines, but little is known about actual outcome of large scale changes in agricultural policy on communities of service-providing organisms. Two data sets containing captures of ground beetles (Carabidae) collected at an interval of 24 years were analyzed; the data were collected in the same area in Sweden under different environmental conditions before and after the introduction of a national pesticide risk reduction program. Environmental changes were analyzed by considering indicators of land use and agricultural management over time. Ground beetles collected over the whole season were considered and species were categorized according to functional traits. Environmental changes between the two time periods were characterized by increases in fallow and organic farming and a strong reduction in the amount of pesticide active ingredients sold and risk factors associated with pesticides. Although there were no changes in ground beetle species richness and community evenness after mitigation of agricultural intensification, there were differences in dominance distribution and functional composition. Ground beetles collected in the 1980s had higher proportions of carnivorous, cursorial, and small and intermediate size beetles than those collected in 2003. Communities sampled in 2003 had increased proportions of omnivorous, mobile, spring breeding, and large beetle species. These shifts in functional characteristics of ground beetle communities may improve biological control of cereal aphids and reduce variability in this ecosystem service over time.

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1. Introduction

Understanding how global change influences species richness and community composition over time in agroecosystems is a major challenge for applied ecological research. Declines over time have been observed for many communities (Robinson and Sutherland, 2002; Thomas et al., 2004), and agricultural intensification has been identified as one of the main drivers of this decline (Tscharntke et al., 2012). To maintain high and stable agricultural production, it is important to follow how communities that provide ecosystem services respond to land use intensification in agroecosystems over time. There is both a need to monitor possible deterioration of ecosystem services caused by agricultural intensification, as well as to assess the long term impact of large scale mitigation efforts and changes in agricultural policies. A serious problem, however, is the lack of long term monitoring data of biodiversity in general and service providing organisms in particular (Dornelas et al., 2013).

During the last 50 years, agricultural landscapes of European countries have undergone substantial intensification characterized by larger field size, simplification and shortening of crop rotations, increased use of agrochemical inputs, and loss of semi-natural habitats (Bennett et al., 2012; Stoate et al., 2001; Tilman et al., 2002). Even if this is the general trend in European agricultural landscapes, agricultural policy history and the degree of intensification over time differ among countries. For instance, Sweden has since the early 1970s had two distinct phases in agricultural policy (Ekström and Bergkvist, 2008; Wretenberg et al., 2007).

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The first phase from the early 1970s to 1987 was a period of strong intensification characterized by a rapid increase in agrochemical inputs and yield per hectare, and a decrease in area of semi-natural habitats. The second phase from 1987 is characterized by a sharp decline in quantities of active ingredients used and an increase in set-aside areas; because Sweden concurrently implemented a set-aside program and a national pesticide risk reduction program (Ekström and Bergkvist, 2008). Recently, several European countries have adopted similar programs (Barzman and Dachbrodt-Saaydeh, 2011). The early adoption of the Swedish mitigation program allows for an examination of how such large scale and long term programs affect communities of ecosystem service-providing organisms.

Several studies have demonstrated a positive relationship between number of species and the rate or stability of various ecosystem functions (Cardinale et al., 2012). Considering the different potential relationships between natural enemy species richness and herbivore suppression (Straub et al., 2008), a recent meta-analysis showed that increasing natural enemy species richness usually leads to higher herbivore suppression in agricultural systems (Letourneau et al., 2009). Such results have led to a focus on changes in species richness due to land use modifications. It is, however, increasingly recognized that community composition in terms of relative abundances and functions, more than just the number of taxonomic units, is an important determinant of ecosystem functioning (Bommarco et al., 2012; Hillebrand et al., 2008). Environmental changes are likely to shape communities according to species life-history traits which, in turn, will affect flow and stability of ecosystem services (Hooper et al., 2005). Moreover, considering both taxonomic and functional diversity provides information on the relative contribution of a species to the sum of ecological functions of the community and on ecosystem resilience (Flynn et al., 2009; Walker, 1995). It is, thus, critical to examine several different facets of community structure to understand the impact of land use change on communities and predict the consequences for ecosystem functions and services.

Ground beetles (Coleoptera: Carabidae) are key generalist predators in agroecosystems consuming various crop pests (Kromp, 1999; Symondson et al., 2002). Ground beetles are a very well studied group of invertebrates and they are often used as bioindicators. It is virtually unknown how mitigation of agricultural intensification affects ground beetle communities and the biological control service they provide over longer time periods.

The aim of this study was to investigate how ground beetles communities react to mitigation of agricultural intensification, using data from two sets of ground beetle sampling in cereal fields separated by 24 years in the Uppsala province in Sweden. This study examines how (i) ground beetle species richness, (ii) community composition, and (iii) functional diversity changed over a period of time characterized by policies mitigating agricultural intensification. It was hypothesized that the mitigation phase would result in communities with higher functional diversity. Differences in taxonomic and trait composition between historic and current communities were also expected as a result of environmental filtering due to changes in agricultural policies.

2. Materials and methods

The study was conducted around the city of Uppsala, Sweden (59°51′ N; 17°38′ E). The landscape of this region is characterized by a mosaic of arable land and semi-natural habitats. The response of carabid communities to mitigation of intensification programs was examined using two datasets of ground beetles sampling collected for different purposes. These two datasets were selected to represent the two phases of agricultural intensification in Sweden as they are based on fields sampled before (Ekbom and Wiktelius, 1985) and after 1987 (Öberg et al., 2007). The samples were taken in the same region, but because the datasets were sampled for different purposes and some fields have been urbanized, it was not possible to select the exact same fields before and after 1987. Thus, among the different sampling sites available, 14 spring cereal fields (i.e., seven fields in each time period) located in the same area were selected; the fields were within the same landscape context and with carabid beetles collected over the entire season in order to ensure that carabid species with different phenologies would be included. Fields sampled before 1987 were all conventional fields, whereas fields from after 1987 were all organic fields. By comparing ground beetles sampled in conventional farming during the intensification period and ground beetles sampled in organic farming after the mitigation period, the present study examines carabid communities in two extreme and contrasting situations in terms of intensification. Within each time period, fields were grouped according to their landscape context because landscape complexity can influence ground beetle communities (Purtauf et al., 2005; Winqvist et al., 2011). Landscape complexity of each field was characterized by computing the proportion of semi-natural habitats within a radius of 500 m using ArcView 10 (ESRI) and data from the National Land Survey of Sweden from 2003. This spatial scale has been found to be suitable for analyzing the effects of landscape context on carabid communities (Maisonhaute et al., 2010). Semi-natural habitats were composed of woodland and pastures. Fields were categorized between simple and complex landscape using 25% semi-natural habitat as a threshold (Table S1). This classification was used instead of continuous landscape variables due to the lack of precise land use data for the 1980s.

2.1. Changes in land use and agricultural management

To describe the changes in land use and farming practices since the adoption of the mitigation plan in 1987, the following variables were selected: land use (arable and semi-natural habitats), sales of pesticides, pesticide risk indicators, proportion of organic farming, use of fertilizers, cereal yields, and areas of fallows and leys. The data were collected from databases on agriculture and environment (Statistics Sweden, 2012a,b), a database on pesticide sales (Swedish Chemical Agency, 2012), and information from Ekström and Bergkvist (2008). Where possible information is presented for the Uppsala province.

2.2. Ground beetle sampling

Ground beetles were sampled from spring cereal (oats and barley) fields using pitfall traps. All sampled fields were ploughed in the autumn of the year preceding sampling. Sampling intensity varied between fields both in terms of number of traps per field and sampling period (Table S1). Number of sampled points per field ranged from 5 to 36. When five points were used, one point consisted of a pair of pitfall traps connected by a plastic barrier (the length of the barrier was 70 cm in the 1980s and 50 cm in 2003). When 36 sample points were used, one point consisted of one pitfall trap. All traps were filled with water and detergent and emptied at least once a week. Distribution of the traps within the field varied between sites with traps either distributed over the entire field, along a gradient from edge toward the center of the field, or more toward the center of the field (Table S1). Prior to analysis, data were standardized between sites by taking into account individuals collected during the same period and pooling the individuals over this period for each site and year. Because of the various sampling efforts and different trap distributions, the absolute abundance was not analyzed.

Table 1
Description of carabid trait groups and categories used in this study and summary of the proportion of each trait category within the 1980s and the 2003 assemblages.

Trait groups	Categories	Code	% of single traits by groups in the assemblages	
			1980s	2003
Body size	1. <6 mm	BS_1	54.6	23.9
	2. 6–10 mm	BS_2	13.1	7.8
	3. >10 mm	BS_3	32.2	68.2
Dispersal	1. Class 1[a]	Disp_1	37.8	11.1
	2. Class 2	Disp_2	31.0	59.3
	3. Class 3	Disp_3	0.9	3.9
	4. Class 4	Disp_4	29.9	25.3
Diet	1. Carnivorous	D_1	85.3	58.1
	2. Omnivorous	D_2	13.2	36.8
	3. Phytophagous	D_3	1.3	4.8
Breeding season	1. Spring[b]	Br_1	14.8	45.4
	2. Autumn	Br_2	85.1	54.4

[a] See methods for explanations about mobility classes.
[b] Variable used in the analysis.

2.3. Functional traits

Information on four traits of ground beetles was collected from the literature: body size, dispersal ability, diet, and breeding season (Table 1). These traits were selected because they reflect differences in functional attributes or ecological strategies, and because they are known to be key traits for understanding carabid responses to disturbance (Barbaro and van Halder, 2009; Ribera et al., 2001). Using wing morphology alone to estimate dispersal ability can be misleading (Hendrickx et al., 2009). Instead the dispersal ability classification described in Hendrickx et al. (2009) was used. Class 1 was mainly composed of cursorial dispersers and included brachypterous, dimorphic, and macropterous species characterized by partially developed wings, or no functional flight musculature. Class 2 was composed of dimorphic and polymorphic species, for which less than 10% of individuals exhibited functional wings or flight musculature. Class 3 was composed of dimorphic and polymorphic species, for which flight records have been reported. Class 4 comprised only of consistently macropterous species with functional flight musculature, and for which flight records have been reported (Table 1).

Changes in functional traits of ground beetles were assessed using two metrics describing complementary aspects of functional composition of communities: community weighted mean traits (CWM) and Rao's quadratic diversity (Garnier et al., 2004; Lepš et al., 2006). These two metrics have been found to provide relevant information on the mean and dispersion of traits within communities (Ricotta and Moretti, 2011). CWM is the average of trait values in the community weighted by the relative abundance of the species with each trait and quantifies potential shifts in mean trait values within communities. The Rao's index is a measure of functional diversity including information on richness and evenness of functional traits within a community and can be used to analyze patterns of trait divergence (Ricotta and Moretti, 2011).

2.4. Data analysis

Linear models were used to investigate patterns of changes in agricultural intensification and land use over the 24 year time period. Quadratic terms were included in the models to account for possible nonlinear relationships. When strong auto-correlation within the residuals was found, first-order autoregressive models (AR1) were used to account for the temporal auto-correlation in the data (Wretenberg et al., 2007; Zuur et al., 2009). The different models were compared using the Akaike Information Criterion.

Effects of time period and landscape context as well as the interaction between these factors on species richness and community evenness were analyzed using two-way ANOVAs for unbalanced data. Species richness was $\log_{10}$-transformed and community evenness was arcsine square-root transformed to meet assumptions about normality and homoscedasticity. Because sampling effort varied across fields and periods, individual-based rarefaction was used to compute a standardized measure of species richness (EcoSim v. 7.72, Entsminger, 2011). Mean species richness in each field was based on rarefaction to 106 individuals (i.e., the minimum number of total individuals collected per field) with 1000 iterations.

Effects of time period and landscape context on species composition and functional trait composition were analyzed with multivariate analysis of variance, using canonical Redundancy Analyses (RDA) with Monte-Carlo tests with 999 permutations (Borcard et al., 2011). Partial Redundancy Analyses were then used to summarize changes in species and functional composition between the two time periods while controlling for the effect of landscape context. Abundance of ground beetles was Hellinger-transformed to reduce the effect of high abundances values in the data matrix (Legendre and Gallagher, 2001) and singletons were removed to eliminate the effects of vagrant species (Moretti et al., 2010).

Differences in beta-diversity, as a measure of variation in community structure among time periods and landscape contexts, were examined using a test for homogeneity of multivariate dispersion based on Morisita-Horn dissimilarity (Anderson et al., 2006). Differences among groups were tested using pairwise permutations of distance to centroid values.

3. Results

Proportions of arable land and semi-natural habitats did not change over 24 years in the Uppsala province (Table S2). The proportion of arable land under organic farming in Sweden increased during this period from 0% in the early 1980s to more than 10% in 2010 (Fig. 1a). The area of fallows in the Uppsala province also increased over this time period, whereas the area of ley and cultivated pastures remained constant (Table S2).

No changes in cereal yield (Fig. 1c) and in amount of nitrogen, phosphorous or potassium sold (Table S2) were detected. The total amount of sold active pesticide ingredients in the country decreased over the time period (Fig. 1b and Table S2). The strong reduction is mainly attributed to the use of lower doses of older pesticides, and the introduction of new low-dose herbicides and insecticides. This also explains the decrease in the environmental and health indicators associated with the use of pesticides over the time period (Fig. 1d).

3.1. Species richness, community evenness and species composition

A total of 32,382 individuals representing 54 species were collected in the 14 fields during the standardized sampling period. Of this total and regardless of sampling effort, 30 species were recorded in both time periods, while 24 species were trapped in only one sampling period. A total of 49 species were recorded in the early 1980s and 35 species in 2003. There was no difference in average rarefied species richness and community evenness between the two time periods (Table 2). There was no effect of landscape context and its interaction with the time period either on species richness or evenness (Table 2).

The composition of carabid communities from each time period differed (Table 3), but landscape context and its interaction with the time period were never significant for species composition (Table 3).

There were no differences in terms of variation in community structure (β diversity) among time periods and landscape context. There were no differences in the average distance among fields within a group to the group centroid in multivariate space (i.e., multivariate dispersion) ($F = 2.537$, $P = 0.11$).

Partial redundancy analysis indicated that the time period accounted for a significant proportion of the variance in species composition (31.5%; $P = 0.002$) (Fig. S1). Several species such as *Patrobus atrorufus*, *Trechus quadristriatus*, *Trechus secalis*, *Loricera pilicornis*, or *Synuchus vivalis* were found in higher proportions in the 1980s than in 2003. In contrast, other species such as *Poecilus cupreus*, *Harpalus rufipes*,
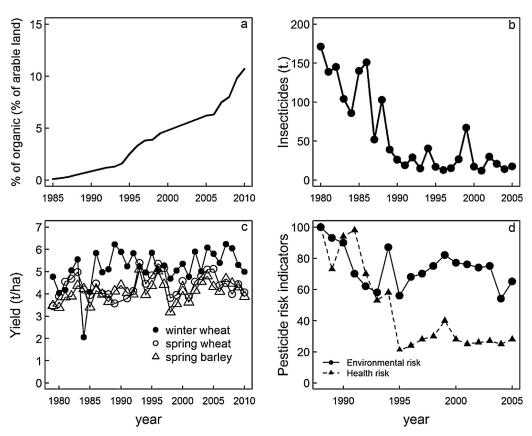
Fig. 1. Changes in agricultural practices and land uses in the Uppsala province (c) and in Sweden (a, b and d) during the intensification (until 1987) and the mitigation (1987–2003) period.

Table 2
Two-way analysis of variance of the effects of time period (1980s and 2003), landscape context (simple and complex) and their interaction, on rarefied carabid species richness and on community evenness.

Factors	d.f.	Species richness		Evenness	
		F	P-value	F	P-value
Time period	1	0.039	0.847	0.353	0.565
Landscape	1	0.459	0.513	1.286	0.283
Time period × landscape	1	0.062	0.808	0.154	0.702

Amara similata, or *Amara aulica* were found in higher proportions in 2003 than in the 1980s (Fig. S1 and Table 4). In the 1980s, *T. secalis*, *T. quadristriatus*, *Pterostichus melanarius*, and *H. rufipes* were the dominant species representing more than 70% of the assemblage whereas the dominant species in 2003 were *P. melanarius*, *H. rufipes*, *P. cupreus*, and *Bembidion lampros* (Table 4).

3.2. Functional traits

There was a significant effect of the time period on community traits composition (CWM) (Table 3), but no effect of landscape context or its interaction with the time period (Table 3).

The time period explained a large proportion of variance in community trait composition (45.8%; $P = 0.002$) (Fig. 2a). There were differences in community composition in terms of diet, body size, breeding season, and dispersal ability (Fig. 2a). Ground beetles collected in the 1980s were characterized by higher proportions of carnivorous, cursorial (class 1), small and intermediate size ground beetles compared to 2003. Communities sampled in 2003 were associated with increased proportions of omnivorous, mobile species (class 2), spring breeders and large beetles compared to the 1980s. The proportions of phytophagous and more mobile (class 3 and class 4) species remained unchanged between (Fig. 2a).

The early 1980s assemblage was dominated by small size carabids, whereas larger beetles dominated in 2003 (Table 1). Analysis of dispersal ability revealed that the early 1980s was dominated by classes 1, 2, and 4, whereas 2003 was mainly dominated by class 2 (Table 1). Communities from both time periods were dominated by carnivores and autumn breeders. However, the relative proportion of spring breeders increased significantly in 2003 compared to the 1980s (Table 1).

An effect of time was found for the functional diversity of trait groups (Table 3). Time period explained a significant proportion of variance in functional diversity (34.7%; $P = 0.003$). The ground beetle communities sampled in the 1980s were more functionally diverse for body size than communities from 2003 (Fig. 2b) revealing a more even distribution in relative proportions of these traits in 2003 (Table 1). In 2003, communities were more functionally diverse for traits associated with breeding season and diet (Fig. 2b). No differences in functional diversity of dispersal ability were found. There were no effects of landscape context or interaction between landscape and time period (Table 3).

Table 3
Two way redundancy analysis with 999 permutations Monte Carlo test on species composition, trait composition (CWM), and functional diversity (FD), for the factors time period (1980s and 2003), landscape context (simple and complex), and their interaction. Levels of significance are provided as footnote.

Factors	d.f.	Species composition		CWM		FD	
		F	P-value	F	P-value	F	P-value
Time period	1	5.651	0.001[***]	8.962	0.001[***]	5.555	0.006[**]
Landscape	1	1.410	0.177	1.599	0.199	0.591	0.594
Time period × landscape	1	0.498	0.836	0.604	0.580	0.429	0.716

[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

Table 4
Proportional abundance of the main species found in ground beetle communities sampled in the 1980s and in 2003.

Species	Relative abundance (%)	
	1980s	2003
Trechus secalis	27.3	3.5
Trechus quadristriatus	19.6	<1
Pterostichus melanarius	17.0	23.3
Harpalus rufipes	8.1	17.5
Bembidion lampros	6.1	13.0
Pterostichus niger	5.3	6.7
Anchomenus dorsalis	5.2	2.4
Synuchus vivalis	4.0	<1
Bembidion quadrimaculatum	1.3	4.2
Calathus melanocephalus	1.1	<1
Poecilus cupreus	<1	17.3
Amara aulica	<1	2.5
Amara similata	<1	1.7
Clivina fossor	<1	1.7
Bembidion guttula	<1	1.2
Trechus micros	<1	1.1
Other spp.	5.1	4.0

4. Discussion

Since the early 1980s, the environmental conditions of the studied region have shifted from a period of significant intensification to a mitigation phase. This change did not affect ground beetle species richness or community evenness. But a significant shift in the dominance distribution among ground beetle species between time periods was found, affecting community and functional composition of the community.

Two species replaced previously dominant ones, thereby affecting functional composition. *T. secalis* and *T. quadristriatus*, decreased between the 1980s and 2003. They are functionally close with regards to diet, breeding period and body size. Both are autumn breeders, carnivorous, and small body size beetles. The two newly dominant species in 2003, *P. cupreus* and *B. lampros*, are both spring breeders and from dispersal class 2. These results suggest that species turnover has not been a random process, but instead a result of species with shared traits reacting to environmental changes. Even though the dataset is limited to two separate time periods, preventing analysis of continuous changes at longer temporal scales, this investigation of changes in ecological traits provides a more mechanistic understanding of how community structure responds to land use changes between these two time periods.

The relative proportion of spring breeders increased in 2003 compared to the 1980s leading to a more even distribution in 2003, and to a more even occurrence of autumn and spring breeders. First, the increased amount of fallows in the landscape can have provided more overwintering sites for spring breeders that usually hibernate as adults in boundary structures or grasslands, while autumn breeders predominantly hibernate as larvae in arable soils (Holland et al., 2009; Weibull et al., 2003). Second, spring breeders may have benefited from lower levels of pesticide pressure resulting in lower mortality rates during dispersal. Reduced tillage favors spring breeders such as *B. lampros* or *Bembidion quadrimaculatum*, whereas autumn breeders such as *P. melanarius* and *T. quadristriatus* are more often found in fields with conventional ploughing (Kromp, 1999). It was not possible to quantify changes in soil management in the Uppsala province, but non-inversion tillage and reduced tillage are increasingly adopted by farmers in Sweden. For instance, in 2010, reduced tillage was applied to about 16% of the area under spring barley whereas it was not adopted at all in the early 1980s (Statistics Sweden, 2012a).

Carnivorous species dominated assemblages in both time periods, but the relative proportion of omnivorous carabids increased considerably from the 1980s to 2003. This shift toward a more functionally diverse assemblage in diet can be explained by several changes in land use. The observed reduction in herbicide pressure, the increased adoption of reduced tillage, and the higher proportions of organic farming and fallows have probably increased the availability of plant material within fields and landscapes for omnivorous and phytophagous species. The proportion of purely phytophagous species in assemblages was very low in both time periods. Although mitigation included decreased intensity in cultivation practices, it did not include re-diversification of the landscape, and the studied agricultural areas remain as fragmented landscapes largely dominated by ephemeral and disturbed habitats. Thus, the observed increase in dominance of omnivorous beetles might be the result of their wider trophic niche breadth and greater resilience to reduction in food supply, enabling them to persist in stochastic environments (Purtauf et al., 2005; Schweiger et al., 2005).

The shift in body size from small size carabids in the early 1980s to large-size carabids in 2003 is in accord with known effects of management intensity on carabid body size. Large-size species are negatively affected by disturbances such as pesticide
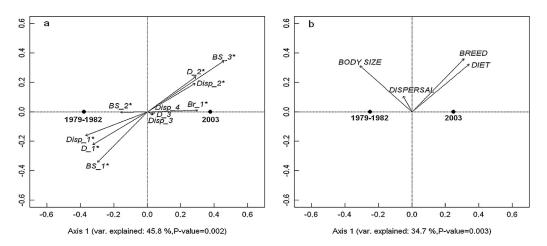

Fig. 2. (a) Partial redundancy analysis summarizing relative changes in the community weighted mean traits of ground beetle communities between each time period (1979–1982 and 2003), while controlling for the effect of landscape context. Centroids of time periods are represented by black dots (for codes see Table 1); * = change in CWM significant at *P* < 0.05. (b) Partial redundancy analysis summarizing relative changes in functional diversity of trait groups of ground beetle communities between 1979–1982 and 2003 (black dots = centroids of time periods; All trait groups were significantly related to time period except dispersal capacity at *P* < 0.05).

applications or soil tillage. Smaller carabids are associated with highly disturbed sites whereas larger carabids are found in undisturbed areas (Blake et al., 1994; Magura et al., 2006; Ribera et al., 2001). Small-sized carabids usually occur in higher densities than large-sized species and have a lower probability of local extinction (Magura et al., 2006). Moreover, larger carabids need more resources, develop more slowly and have lower reproductive rates compared to smaller species, and are therefore more sensitive to temporal variability in resource availability (Blake et al., 1994; Ribera et al., 2001).

Dispersal ability is often regarded as a predictor of species sensitivity to habitat fragmentation and disturbance (Henle et al., 2004). Theory predicts a restricted occurrence of species with poor dispersal abilities in highly fragmented landscapes or disturbed habitats. Surprisingly, it was found that the overall proportion of individuals with low dispersal abilities (i.e., class 1 and class 2) and good dispersal ability (i.e., class 3 and class 4) was similar over time, and that poor dispersers dominated in both time periods. This advantage to poor dispersers might be due to mortality during dispersal, or because of interactions with other correlated traits (Barbaro and van Halder, 2009; Henle et al., 2004).

Recent studies have suggested that structurally complex landscapes support higher levels of biodiversity and ecosystem services compared to simple landscapes because they can provide key resources for a range of organisms (Tscharntke et al., 2012). In contrast the results reported here indicate no effects of landscape complexity on ground beetle communities either in an intensified or a mitigated context. The influence of landscape context for ground beetle assemblages has been found to range from little or no influence to a strong effect (Maisonhaute et al., 2010; Schweiger et al., 2005; Winqvist et al., 2011). Many factors such as soil characteristics, within-field plant diversity, soil tillage, and non-crop habitats in the surrounding environment affect ground beetles and this could explain these variable results (Holland and Luff, 2000).

The main limitation of the present study is that communities from conventional fields in the 1980s were compared to communities from organic fields sampled in 2003. Thus the farming system effect is confounded with the time period effect. However, despite this limitation the data provide relevant information about how service-providing communities react to mitigation programs which are, by definition, multi-factorial. First of all, several studies, including a study performed in the Uppsala province, demonstrated that farming systems have little or no influence species richness and activity density of ground beetles (Melnychuk et al., 2003; Purtauf et al., 2005; Winqvist et al., 2011). Secondly, promoting organic farming is an important part of the mitigation program in Sweden. Thus, the changes in community structure highlighted in this study are relevant in the context of assessing the overall effect of the mitigation program even if the main drivers of these changes cannot be identified. The differences in taxonomic and functional composition found in the present study can be interpreted as resulting from changes in agricultural policies including the promotion of organic farming. Despite these shortcomings, comparing historic and modern community data sampled in the same regions (e.g., Bommarco et al., 2012) is a promising approach that should be possible to adopt for more regions and taxa; especially given the lack of continuous monitoring of biodiversity in general and beneficial organisms in agricultural landscapes in particular (Dornelas et al., 2013).

Although mitigation programs have not increased species richness or evenness of ground beetle communities, changes in dominance distribution and functional composition of ground beetles were found following changes in environmental conditions. These large scale changes can have profound impacts on ecosystem functioning and the delivery of ecosystem services. First, the higher proportion of spring breeders found during the mitigation period can be beneficial for pest control services in cereals. Spring breeders colonize cereal fields early in the season. High numbers of generalist predators during aphid colonization increase the probability of controlling aphid populations. Second, the increased proportion of omnivorous carabids after the mitigation period may have ambivalent effects on cereal pest control. In the short term, a higher proportion of omnivores could reduce the biological control of herbivores as it can weaken the strength of predator–prey interactions (Frank et al., 2011). On the other hand higher proportions of omnivores could also enhance natural pest control, and reduce its variability, in the long-term if alternative prey and food are available during periods where pest populations are low (Symondson et al., 2002). Finally, the switch in body size distribution between time periods from communities dominated by small-size carabids in the 1980s to more diversified carabid communities (in terms of body size distribution) can lead to increased intraguild predation and therefore reduced biological control (Prasad and Snyder, 2004). Maintaining biodiversity and the flow of ecosystem services delivered to agroecosystems will require a more mechanistic understanding of the links between agri-environmental policies, community structure and ecosystem functioning.

Acknowledgements

Appendix A.   Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.05.014.

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