

Multi-scale effects of agri-environment schemes on carabid beetles in intensive farmland



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ABSTRACT

Agri-environment schemes (AESs) were implemented to reduce the loss of biodiversity in agro-ecosystems. This study aimed to assess whether AESs at either local or landscape scale increase the carabid abundance-activity and species richness. Carabids were sampled in 496 fields in a 430 km² study area of central-western France. Based on the extensiveness of the agricultural practices involved, the different AES types were aggregated into three categories (AES_{EXT+}, AES_{EXT++} and AES_{EXT+++}) forming a gradient of extensiveness in farming practices. We sampled 20 fields in each of the three AESs categories. Each AES fields was paired with conventional fields. A series of statistical models were built to test the balance between the effects of AESs on either the carabid abundance-activity or species richness. AESs affected carabid abundance-activity and species richness both locally and at landscape scale (local characteristics having a greater effect than landscape composition). Carabid diversity benefited from AESs only when the most extensive practices were implemented, i.e. organic farming in cereal crops and delayed cutting in alfalfa. In addition, the local effects of organic farming and delayed cutting coverage interacted positively with these AESs at landscape scale. These results demonstrate that non-targeted organisms can benefit from AES management. They further emphasize the need to consider both local and landscape conditions when studying the effects of AESs on biodiversity. As only the most extensive practices had significant effects at both local and landscape scales, management must be planned strategically in space to ensure that AESs are distributed within the landscape to amplify their positive effects.

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1. Introduction

Major changes have altered European agricultural landscapes since the Common Agricultural Policy (CAP) aimed to increase food production (Godfray et al., 2010; Pe'er et al., 2014). While crop yields have been improved by generalised use of fertilisers and pesticides (Tilman et al., 2002), there has been a significant loss of biodiversity and negative environmental impacts (such as soil erosion, water pollution) in farmland landscapes (Geiger et al.,

2010; Robinson and Sutherland, 2002; Tschardt et al., 2005). Agri-Environment Schemes (AESs) were introduced by the European Union in 1992 (Henle et al., 2008) to counter such negative environmental impacts. AESs provide financial incentives to farmers in order to promote the adoption of environmentally friendly farming practices adapted to each region (Kleijn et al., 2006a; Whittingham, 2007). Agreements covered by AESs include various intensity reduction measures including management of low-intensity pasture systems, integrated farm management, organic farming, conservation of high-value habitats and conservation of target flagship species (Peach et al., 2001; Perkins et al., 2011).

Evaluating the effect of AESs on taxonomic functional biodiversity is of critical importance in order to promote and increase the effectiveness of AESs (Whittingham, 2007). AESs have been reported to significantly enhance biodiversity (Bengtsson

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et al., 2005; Hole et al., 2005; Kleijn et al., 2006b; Kleijn and Sutherland, 2003). This influence however seems to vary depending on the taxa of interest and the studies. Some studies failed to detect any effects of AESs on biodiversity while other studies detected a decrease of biodiversity (Bradbury and Allen, 2003). The effect of AESs on biodiversity may also be influenced by the characteristics of the landscape, such as composition and configuration (Fuentes-Montemayor et al., 2011; Smith et al., 2010), and heterogeneity (Whittingham, 2011) at various scales. Indeed, AESs located in heterogeneous landscapes and in areas supporting high levels of biodiversity are likely to yield greater benefits than those in more homogeneous landscapes (Concepción et al., 2008). Consequently, studies should consider both field and landscape scales in order to give a more balanced and a more relevant assessment of the effects of AESs on biodiversity (Tuck et al., 2014). However, little research has been undertaken yet to determine the effects of the different AESs at landscape scale compared to their local effect (Henckel et al., 2015).

This study used carabids to assess whether AESs increase species abundance and species richness in farmlands. Carabids are known to be highly sensitive to changes in habitat (Magura et al., 2004; Melnychuk et al., 2003). Carabids are not directly targeted by any AES in France, except as a food resource for birds (Vickery et al., 2004). They are potentially important components of functional biodiversity in agro-ecosystems, either as natural enemies of pests or as components of trophic chains sustaining biodiversity (Thiele et al., 1977). In addition, an increase in beetle abundance or species richness may improve ecosystem resilience (Hooper et al., 2005). Crop pest consumption by carabids was found to be positively correlated to prey abundance (Menalled et al., 1999), while species richness may improve community functional resilience as well as biodiversity conservation (Tilman, 1996; Woodcock et al., 2014). Agricultural practices such as tillage or pesticide use have been shown to affect carabid abundance either directly, through mortality and emigration, or indirectly, by changing local microhabitat conditions (Cole et al., 2002; Hatten et al., 2007; Kromp, 1999). A recent meta-analysis comparing organic and conventional practices (Tuck et al., 2014) showed that organic farming had an overall positive effect on arthropods including carabids, although results varied between studies (Eyre et al., 2012; Garratt et al., 2011; Hole et al., 2005).

We evaluated the effect of a broad set of AESs on carabid abundance-activity and species richness in a study area (430 km²)

located in central-western France. Half of this study area was designated as a NATURA 2000 site (since 2003). In 2010, there were agreements in 10 different AES contract types implemented in our study area. The variety of AES types and the large area under contract (over 9000 ha) allow investigating the effects of AESs at local (field) and landscape scales, while taking into account the local environmental factors and landscape structure as in previous studies (Concepción et al., 2012, 2008). We classified AESs a priori, according to their degree of extensiveness (in terms of farming practices), and analysed, in addition to AES effect at local scale, the landscape structure at different spatial scales and the possible influence of AES present in the landscape. Consequently, the aims were (i) to quantify the local effect of the different categories of AESs (AES_{local}) on carabid diversity; (ii) to determine whether the age of AES and the landscape structure modulate the effect of AES_{local} and (iii) to determine whether the area covered by AESs at landscape scale (AES_{landscape}) interacts with the local effects on carabid diversity.

2. Materials and methods

2.1. Study area and AES classification

The study was conducted in the LTER Zone-Atelier “Plaine & Val de Sèvre” which covers an area of about 43,000 ha in central-western France (46.11°N, 0.28°W). This is an agricultural area with about 12,500 fields mainly used for the production of cereals (wheat: 36.38% ± 0.41 of the total area—mean value ± SD in 2009–2010). Perennial crops represented 11.44% ± 0.03, including alfalfa (3.14% ± 0.02) and grassland (8.30% ± 0.02). Land use has been recorded annually since 1995 and mapped onto a GIS (ArcGis 9.3—ESRI Redlands, CA, USA). Since 2004 a large number of agri-environment measures of various types have been implemented in the entire study site by the CNRS research laboratory of Chizé (Bretagnolle et al., 2011), covering up to one third of the study area (in 2013). Overall, 10 different types of AESs have been implemented (see Table 1 for details) and were compared to conventional management.

Based on the extensiveness of the agricultural practices involved, the different AES types were aggregated into three categories for each category of crop (AES_{EXT+}, AES_{EXT++} and AES_{EXT+++}, Table 1; see also (Brodier et al., 2014)), creating a gradient of

Table 1
Average characteristics (mean ± standard deviation) of AESs implemented, their categories and the mean carabid diversity per field.

Practices	AES category	Number of fields sampled	Field area (ha)	AES age (years)	Carabid abundance-activity	Carabid species richness
Conventional (no AES)	Conventional	Wheat: 147 Alfalfa: 64 Meadow: 46	Wheat: 5.9 ± 4.6 Alfalfa: 2.9 ± 1.4 Meadow: 2.7 ± 2.8	–	Wheat: 64 ± 123 Alfalfa: 61.4 ± 78.8 Meadow: 10.4 ± 13.2	Wheat: 7.4 ± 3.5 Alfalfa: 8.0 ± 4.0 Meadow: 3.9 ± 2.7
Reduction of herbicides Reduction of fertilisers Reduction of herbicides and fertilisers	AES _{EXT+}	57	4.7 ± 2.5	3.0 ± 09	50.6 ± 46.8	75 ± 3.7
no-tillage	AES _{EXT++}	52	5.9 ± 4.3	5.1 ± 0.7	50.5 ± 78.9	7.41 ± 3.4
Organic farming	AES _{EXT+++}	35	5.6 ± 3.8	2.4 ± 1.7	98.6 ± 107.5	9.6 ± 4.4
Arable reversion to meadow	AES _{EXT+}	Alfalfa: 34	Alfalfa: 3.8 ± 7.1	Alfalfa: 3.5 ± 1.1	Alfalfa: 60 ± 100.1	Alfalfa: 8.0 ± 4.1
Arable reversion to alfalfa	AES _{EXT+}	Meadow: 9	Meadow: 2.9 ± 1.5	Meadow: 3.0 ± 1.4	Meadow: 20.1 ± 36.4	Meadow: 4.0 ± 3.3
Low-intensity meadow management	AES _{EXT++}	Alfalfa: 5 Meadow: 13	Alfalfa: 2.3 ± 2.2 Meadow: 2.4 ± 1.9	Alfalfa: – Meadow: 4.5 ± 1.0	Alfalfa: 27.8 ± 23.3 Meadow: 11.2 ± 12.3	Alfalfa: 6.8 ± 4.2 Meadow: 4.0 ± 2.3
Delayed cutting Set-aside	AES _{EXT+++}	Alfalfa: 10 Meadow: 24	Alfalfa: 3.4 ± 3.0 Meadow: 1.8 ± 1.2	Alfalfa: 4.7 ± 1.2 Meadow: 4.7 ± 0.9	Alfalfa: 94 ± 87.4 Meadow: 8.3 ± 11.2	Alfalfa: 9.1 ± 4.2 Meadow: 3.8 ± 2.2

extensiveness in farming practices. The order of categorisation reflects an a priori positive effect on carabid diversity.

For annual crops, the first set of crop management (AES_{EXT+}) included three schemes aimed primarily at improving water quality in intensive arable land by the reduction of agrochemical inputs. These schemes required a progressive reduction of herbicide application of around 50% over 5 years (target of 30% reduction by year 3) and/or limitation of fertiliser application to 120 units of nitrogen per hectare per year. Reduced soil disturbance (AES_{EXT++}) included AESs promoting conservation tillage (e.g. harrowing only to a depth of 5–10 cm), in order to prevent soil destruction. Annual crop organic farming (AES_{EXT+++}) included two schemes to subsidise the conversion to and maintenance of organic farming. The quality of the habitats should be improved by the ban on agrochemical inputs (pesticides, herbicides and mineral fertilisers) and limitation of organic fertilisers to 120 units of nitrogen per hectare per year.

For grasslands (i.e. meadows and alfalfa crops), arable reversion (AES_{EXT+}) included two schemes, one for reversion to alfalfa and one for reversion to meadow, with no particular constraints on management. Low intensity management of grassland (AES_{EXT++}) included both grassland and alfalfa and included low inputs. Delayed cutting (AES_{EXT+++}) included two schemes, one for alfalfa and grass/legume mix, with no cutting from 15 May to 31 July (delayed cutting), and one with set-aside grassland, not to be used for any form of farming from 15 May to 31 August. Both schemes included a ban on the use of herbicides and fertilisers.

2.2. Sampling design and carabid identification

To compare the effects on carabid diversity of conventional management and the various types of AESs, 496 fields were sampled (total area 2300 ha, corresponding to 5.4% of the study area: see Table 1). 20 fields of each AES category were sampled: when the number of fields available in an AES category was no more than 20, all fields were sampled. When more than 20 fields were available, 20 fields were randomly selected. The AES fields were as far as possible paired with a conventional field, selected to have the same crop, a similar area and be at less than 500 m from the AES field. Each field was sampled once in 2009 or 2010 (May to early July; Fig. 1). The sampling was stratified by crop type, including wheat, alfalfa and meadow, and by AES category (Table 1).

Carabids were sampled using pitfall traps, a standard method which is easy to implement and provides high capture rates (Luff, 1975). These traps cannot, however, be used to estimate the carabid abundance directly but rather carabid abundance-activity as the traps cannot distinguish between abundance and activity (movements of carabids). Carabid abundance-activity and species richness have been estimated during the spring and early summer when they are active (Thiele et al., 1977). In each field, three pitfall traps were set up within the field (less than 15 m from the field margin and 10 m from each other). Traps were filled with a 50% solution of ethylene glycol. Pitfall traps were left in place for five days. The carabids were stored in the laboratory in a 96% ethanol solution and identified at species level as described by (Jeannel,

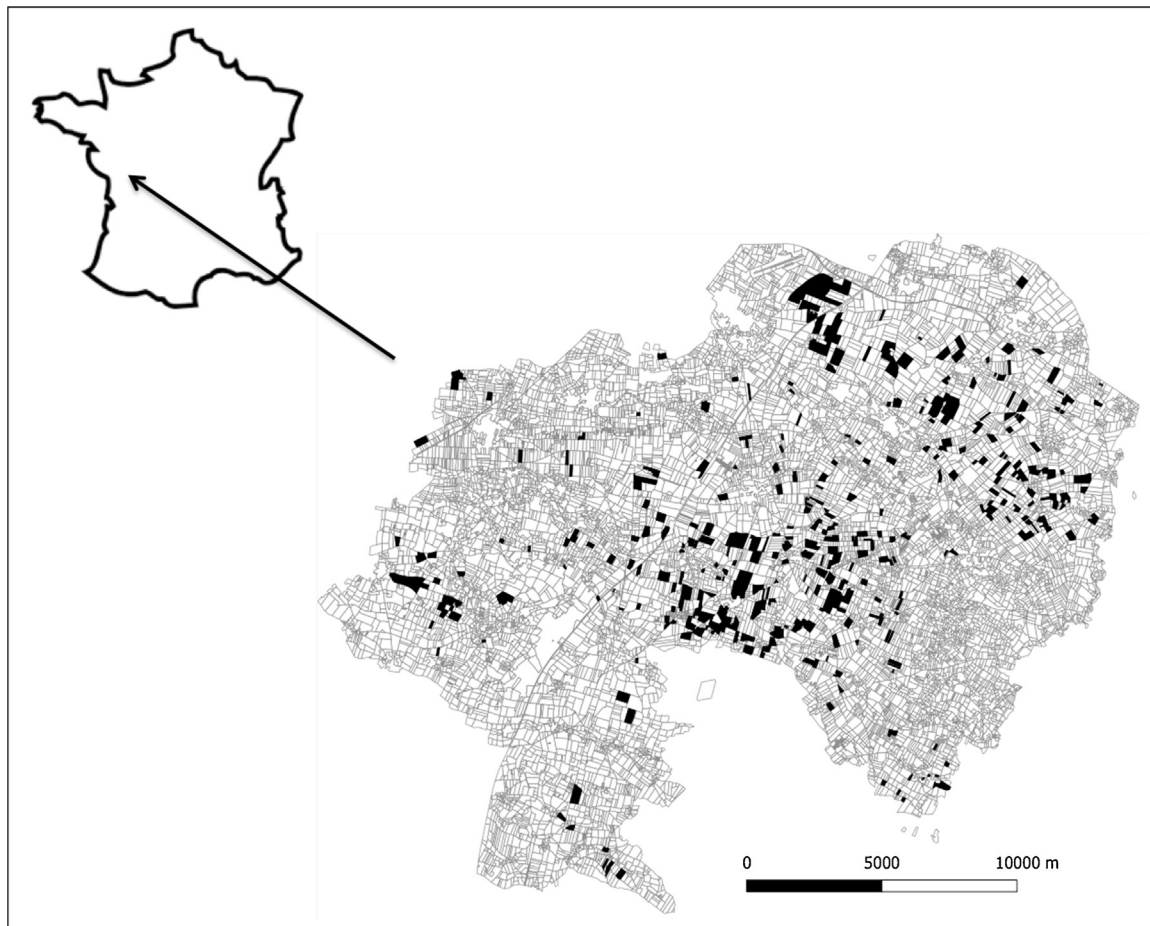


Fig. 1. Map of the study area, the LTER "Zone Atelier Plaine & Val de Sèvre". Sampled fields are indicated in black.

1941). Species abundance–activity and richness were aggregated within each sampled field for analyses.

2.3. Landscape variables

Since landscape composition has been shown to affect the effect of AESs (Concepción et al., 2008), a quantitative description of the landscape around each field was produced, starting from the centroid of each field and moving out in nine concentric buffers, from 200 m to 1000 m radius, with a step of 100 m, using QUANTUMGIS 2.2 (Quantum, 2013). The maximum distance was set at 1000 m because the outer buffers tended to overlap beyond, reducing the statistical independence between samples. However, this extent is much greater than generally considered in such studies on carabids, often up to 500 m (Aviron et al., 2005a; Maisonhaute et al., 2010a; Weibull et al., 2003a). We tested these nine spatial scales in order to know which scale had the most relevant effect on carabid communities. Nine landscape descriptors were calculated for each buffer (always excluding the field being sampled). The first set of five landscape descriptors described the landscape composition (the areas of wheat, meadow and alfalfa), the Shannon's index of crop diversity and the total length of hedgerows within each buffer. The AESs implemented at landscape scale were quantified as a second set of four landscape descriptors, one for the area of each AES category (AES_{EXT+} to AES_{EXT+++}) and one for the total AES landscape area (obtained by pooling all AES categories). We checked the correlation of each landscape descriptors at each distance by using Pearson's correlation, and did not find any correlation coefficients >0.1, thus colinearity was not an issue.

2.4. Statistical analyses

Because of the large number of independent variables that could influence carabid diversity (at both field and landscape scales), all variables were not all included in a single model. Rather, a sequential set of a priori models of the likely mechanisms of species responses to a specific set of variables was selected using an information-theoretic approach (Burnham and Anderson, 2002; Henckel et al., 2015). Carabid abundance–activity and species richness were modelled separately as the response variables. Linear models (LM) were used for log-transformed carabid abundance–activity and generalised linear models (GLM) for a Poisson distribution of carabid species richness. We constructed the model following six steps (detailed below), each step complexifying the model and testing the effect of a set of specific variables (ESM 1). At each step, the best model was selected by comparing AIC values between all possible sub-models using a stepwise deletion procedure and the combination of variables of this best model was retained for the next step. All analyses were performed using the R *vegan* (function *pairwise.t.test*) and *car* (function *Anova*) packages (Fox and Weisberg, 2010; Gentleman et al., 2009; Oksanen et al., 2007). The procedure of model construction is described below (see ESM 1).

2.4.1. Testing the effect of AES at the field scale

As a preliminary first step, the sampling covariates (variables that might affect sampling) were included in the model, i.e. the Julian Day (JD, with day 1 being the first day of the current year; we considered the first and second order to allow for non-linear seasonal variation), year and the interaction between year and JD. In step 2, field descriptors were added to the resulting model of step 1. Field descriptors included field perimeter, soil type (five types: superficial, intermediate and deep calcareous soils and intermediate and deep red soils) and crop type (three types: wheat, alfalfa and meadows). In step 3, the AES category (four categories:

conventional and AES_{EXT+} to AES_{EXT+++}) and their interaction with crop type were added to the variables selected in step 2. In step 4, the AES age was added in two-way interaction with the AES categories and crop type to the variables selected in step 3.

Finally, in step 5, the five landscape descriptors (related to landscape composition and structure) presented above were added. A different model was used for each landscape scale. Each of these models contained the local variables selected in step 4, the landscape descriptors calculated for each landscape scale (from 200 m to 1000 m in steps of 100 m) and all interactions with AES_{local} (i.e. the AES category of the sampled crop). Hence, nine models for carabid abundance–activity and nine for carabid species richness were compared using AIC. As proposed by Ricci et al. (2009), the scale with the lowest AIC was the most relevant spatial scale, which was then used to build the final model. The spatial auto-correlation of model residuals was also checked by using the R function *variog* (Cressie, 1992). No such autocorrelation was found (results not shown). The robustness of the final model was checked by calculating R² between the observed and the predicted values following the method described by Piñeiro et al. (2008). Finally, the significance of each variable in the final models was tested and the likelihood ratio (LR) associated with each variable was calculated using maximum likelihood ratio tests (Type II Wald chi-squared tests) (Fox and Weisberg, 2010). The LR indicates the part of the variance explained by each variable, making it possible to establish a hierarchy among variables. Pairwise post-hoc comparisons were then performed to assess differences between crop types and between AES categories for final model predictions. Significance values were assessed using the Bonferroni correction for multiple comparisons (Sokal and Rohlf, 1995).

2.4.2. Testing the effect of AESs at landscape scale

The balance and interaction between the effects of AESs at local and landscape scales on carabid abundance–activity and species richness was finally tested in step 6. In order to clarify the comprehension by avoiding interactions of four variables, one model per crop type was built. The effect of AESs at landscape scale and their interaction with AES_{local} were assessed by adding the total AES area at a given landscape scale (hereinafter, referred to as AES_{landscape}) to the final model described above. AES_{landscape} was tested at buffers varying from 200 m to 1000 m (one model was run for each buffer). Models including the interaction between the effects of AESs at local and landscape scale, were run for each AES category (three models for AES_{EXT+} to AES_{EXT+++} and one for the model total AES_{landscape}). Then, for each buffer radius, we extracted the AES_{local} coefficient, the AES_{landscape} coefficient and the interaction coefficient between AES_{local} and AES_{landscape}. The coefficients were plotted against the buffer radius to describe spatial trends (with increasing distance) in the balance between the local and landscape effects of a given AES type.

3. Results

26,427 carabids belonging to 94 species were captured during the two years of the study (see Table 1). For both abundance–activity and species richness, all local variables tested (except the field perimeter for carabid abundance–activity) and only the hedgerow length and the diversity of crops (ie Shannon's index) at 500 m were included in the final models (Table 2; see ESM 1 for model construction procedure). The relation between the predicted values from the final models and the observed values gave R² = 0.38 for carabid abundance–activity and 0.40 for carabid species richness, indicating a reasonable model fit. The local variables (the crop type, the AES category and the soil type) had the highest LR values (Table 2).

Table 2
Final selection of local and landscape scale variables for the effects on carabid abundance-activity and richness. Values and significance of Type II Wald chi-squared tests of variables selected for the final models (hedgerow length and the Shannon diversity index for the crops within a 500 m radius).

		Df	Likelihood Ratio for carabid abundance-activity	Likelihood Ratio for carabid species-richness
Local variables	Julian Day	1	41.436 ***	77.547 ***
	Year	1	15.379 ***	15.353 ***
	(Julian Day) ²	1	7.658 **	38.585 ***
	Field perimeter	1	–	ns
	Soil	4	32.156 ***	45.467 ***
	Crop	2	57.998 ***	133.312 ***
	AES type	3	ns	17.960 ***
	AES age	1	ns	7.852 **
	Crop : AES type	6	ns	ns
	Crop : AES type : AES age	7	20.241**	24.070 **
Landscape variables	Crop Shannon diversity	1	ns	4.226 *
	Hedgerow length	1	7.887 **	ns

– indicates variables not selected (Likelihood Ratio columns) in the final model.

* indicates a significant effect on the response variable (carabid abundance-activity or species richness): * : $p < 0.05$, ** : $p < 0.01$; *** $p < 0.001$.

“ns” indicates a selected variable which is not significant.

There is a “:” between two variables when the interaction between the two variables is modelled.

3.1. Local effect of AESs on carabid abundance-activity and diversity

The AES category had a significant effect on carabid diversity in both wheat and alfalfa (Fig. 2). For each crop individually, post-hoc pairwise comparisons between the three AES categories and conventional crops indicated that carabid abundance-activity was significantly higher for AES_{EXT+++} than for conventional management for both wheat and alfalfa ($p < 0.01$, $t = -4.5$ and -2.5 respectively for wheat and alfalfa; Fig. 2), while carabid species richness was significantly higher in AES_{EXT+++} than for conventional management only in wheat ($p < 0.01$ and $t = -4.7$; Fig. 2). There was no significant difference between conventional management, AES_{EXT+} and AES_{EXT++}, indicating that reducing inputs and soil tillage in wheat or reverting from annual crop to alfalfa or meadow did not improve carabid abundance or richness (this could be expected since recent alfalfa and meadows were managed conventionally). The AES age was included in the final model via its interaction with both crop and AES category but this resulted from a single significant interaction between AES_{EXT+} and its age in wheat for both carabid abundance-activity and species richness

(ANOVA, $p < 0.05$, $t = 3.5$ and 3.7 respectively for carabid abundance-activity and species richness; ESM 2).

3.2. Effect of landscape complexity on carabid abundance-activity and diversity

Landscape composition within a 500 m radius gave the lowest AIC among all scales tested for carabid abundance-activity and species richness models (ESM 3), but only the hedgerow length and the Shannon diversity index for the crops were selected for both carabid abundance-activity and species richness. The hedgerow length had a significant negative effect on carabid abundance-activity (ANOVA, $p = 0.005$ and $t = -2.8$; see ESM 4) while the Shannon's diversity index for the crops had a significant negative effect only on carabid species richness (ANOVA, $p = 0.009$ and $t = -2.6$; see ESM 4).

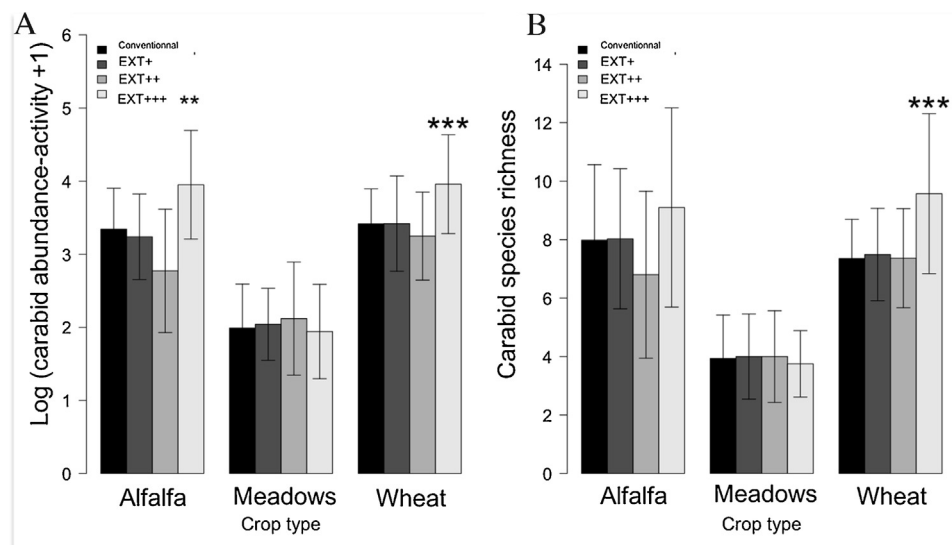


Fig. 2. Final model (with the local variables selected, the hedgerow length and the Shannon diversity index for the crops within a 500 m radius) predictions of A) carabid abundance-activity (log transformed) and B) carabid species richness (mean \pm standard deviation) in the three crops sampled. Asterisks indicate a significant difference for one AES category compared to the conventional management in the same crop; significance values were assessed using pair-wise comparison with the Bonferroni correction (*: p -value < 0.05 , **: p -value < 0.01 , ***: p -value < 0.001).

3.3. Landscape scale influences of AESs on the local effects of AESs

Since only AES_{EXT+++} had a significant effect on both carabid abundance-activity and species richness, additional analyses were limited to fields sampled of this AES category. The effect of $AES_{EXT+++}+landscape$ was assessed for each of the three crop types in separate models. In alfalfa, the local positive effect of AES_{EXT+++} was amplified by $AES_{EXT+++}+landscape$ for both carabid abundance-activity and species richness (Fig. 3a and b), although the interaction between local and landscape scales was significantly positive only at the large spatial scales. In wheat, the local positive effect of AES_{EXT+++} was amplified by $AES_{EXT+++}+landscape$ for both carabid abundance-activity and species richness (Fig. 3c and d), although the interaction between local and landscape scales was positive only at the smaller spatial scales. Finally, in meadows, the local AES_{EXT+++} effects and their interactive effects with the $AES_{EXT+++}+landscape$ were opposite and non-significant for carabid abundance-activity or species richness: $AES_{EXT+++}+landscape$ diminished the local effect of AES_{EXT+++} on carabid abundance-activity, while the opposite was found for carabid species richness (ESM 5).

4. Discussion

4.1. Effect of AESs at local (field) scale

Carabid abundance-activity and species richness were both higher in organic wheat and delayed cutting alfalfa fields (AES_{EXT+++}) than in fields with the same crops but managed conventionally. The results are consistent with Tuck et al. (2014), who found an average increase in arthropod species richness of about 25% using organic farming methods rather than conventional farming. Our model predicted an average increase in carabid species richness of 20.2% and 11.7% in respectively wheat crops and in alfalfa. Other AESs, such as reducing soil tillage or nitrogen input, were not beneficial to carabids. Only the most restrictive AESs seem to have detectable effects on carabid beetles. These results possibly indicate the existence of a threshold effect for the AESs or a limitation of AESs aggregation (Puech et al., 2014). Carabids responded in the same way (and nearly to the same magnitude) to organic farming in wheat and delayed cutting in alfalfa. There is no obvious ecological link between the predicted effects of these two practices on carabids. One explanatory mechanism may involve

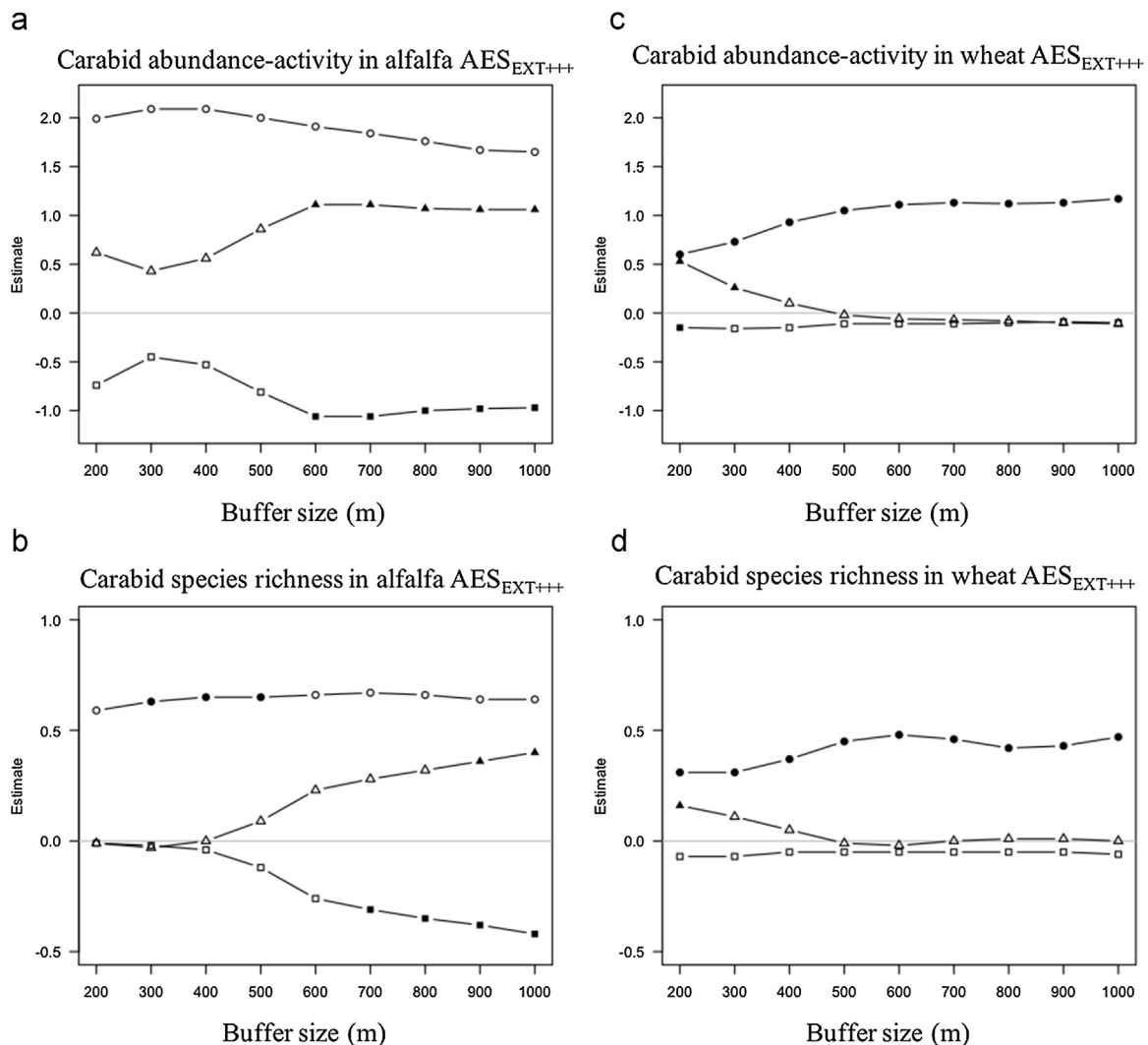


Fig. 3. Modelled effects for different spatial scales with the local effect of AES_{EXT+++} (dots), the area of AES_{EXT+++} in the landscape (squares) and their interaction (triangles). The first line shows the modelled effects for the carabid abundance-activity model, the second line shows the modelled effects for the carabid species richness model. (a) effects of landscape area under AES_{EXT+++} on carabid abundance-activity in alfalfa AES_{EXT+++} ; (c) effects of area surface under AES_{EXT+++} on carabid abundance-activity in wheat AES_{EXT+++} ; (b) effects of landscape area under AES_{EXT+++} on carabid species richness in alfalfa AES_{EXT+++} ; (d) effects of landscape area under AES_{EXT+++} on carabid species richness in wheat AES_{EXT+++} . Solid symbols represent significant variables (i.e. $p < 0.05$ in LM for carabid abundance-activity and GLM with a Poisson distribution for carabid species richness). The grey horizontal line represents 0.

weed diversity and/or abundance, since weeds are more abundant in wheat under organic farming (Tuck et al., 2014; Henckel et al., 2015), and also in alfalfa with delayed cutting (Badenhausser et al., 2008). The increase in the number of weeds in organic farming is likely related to the bans on the use of pesticides and/or synthetic nitrogen fertilisers. No comparable effects were detected in carabids for AES_{EXT+} in wheat (reduction in nitrogen and/or herbicide inputs) or in meadow (nitrogen reduction). These results suggest that these practices are not sufficient to induce an increase of weed abundance or richness (to the extent that carabid abundance-activity and richness also increase with weed diversity). Only a complete ban of pesticide or a different soil tillage may therefore have some effect on carabid beetle diversity and abundance.

There was no sign that AESs had any effect in meadows. Carabid abundance-activity and species richness were the lowest in meadows. This result suggested that meadows may be a poor habitat for carabids. Alternatively, vegetation in meadows could reduce the effectiveness of pitfall traps through the decrease of carabid activities and/or through the higher complexity and density of vegetation, making carabids less likely to be caught (Lang, 2000; Thomas et al., 2006). Furthermore, AES_{EXT++} in meadows may not have improved the meadow quality, as there were no major land management requirements. For instance, the maximum permitted fertiliser input was actually higher than the current average input. However, AES_{EXT+++} had surprisingly no effect in meadows but a very strong effect in alfalfa. This result may have been due to the fact that AES_{EXT+++} in meadow (i.e. set-asides) consisted only in prohibiting harvesting (rather than delaying cutting), possibly degrading the quality of the habitat for carabids. Alternatively, carabid communities in meadows may have responded in autumn rather than spring because weeds in meadows may grow later than in alfalfa. Only spring breeding species were captured in this study since all samplings occurred during spring.

4.2. Local effects versus effects at landscape scale

The local variables (crop and management type, i.e. AES vs. conventional) had a greater effect on carabid diversity than the landscape variables. These results concord with the conclusions reached by Tuck et al. (2014). For both carabid abundance-activity and species richness, the LR values of local variables were always higher than for the landscape variables. This significant local effect also concurs with previous studies (Purtauf et al., 2005; Weibull et al., 2003b), and may be due to environmental filters linked to habitat selection (Myers and Harms, 2009; Schweiger et al., 2005). In our study, the greatest effect on the carabid community was 500 m, which concurs with several other studies (Aviron et al., 2005b; Judas et al., 2002; Maisonhaute et al., 2010b). Although Concepción et al. (2012) suggested that there was an interaction between the landscape and local contexts and predicted that increasing the complexity of the landscape might increase the local effects of AESs, no such effect was found in our study. Possibly because the range of variation in landscape complexity was too limited (Bengtsson et al., 2005; Henckel et al., 2015).

4.3. The balance between local and landscape scale effects depending on crop type and AES

Organic farming practices in wheat (AES_{EXT+++}) had a strong positive local effect on both carabid abundance-activity and species richness. This local effect was further increased when organic farming practices were used at landscape scale, in particular at smaller scales (i.e. at lower distance buffers). For alfalfa, the effects of AES on carabids were to some extent similar to those detected in wheat. The strong positive local effect of delayed cutting was

amplified by the presence of AES_{EXT+++} in the landscape, especially at large spatial scales, for both carabid abundance-activity and species richness (Fig. 3b and e). Carabid abundance-activity and species richness were always much lower in meadows, a situation that was not improved at local scale by any AES_{local} category.

5. Conclusion

Similarly to positive effects detected for weeds (Henckel et al., 2015), we found that only extreme changes in farming practices may enhance biodiversity (Kleijn et al., 2006b; Kleijn and Sutherland, 2003). Only cereal fields under organic farming or delayed cutting alfalfas benefited to carabid diversity, despite the fact that these practices strongly differ from each other. However, both represented the highest levels of constraints and change in comparison to conventional management. We therefore suggest that the magnitude of change (or constraint) is the most important factor of AES implementation to increase carabid diversity. In addition, specific implementation strategies for AESs may be warranted to increase either bio-control services or community persistence. It is important to support a high diversity of management types in order to maintain and increase species diversity at landscape scale (Di Giulio et al., 2001; Loreau et al., 2002). Our results further emphasise the need to consider both the local and landscape context at different scales when studying the effects of AES on biodiversity. They show that in most cases local effects have a greater effect than landscape effects. However, both scales interacted, amplifying the positive local effects (e.g. in cases of organic farming or delayed cutting). These results provide important guidelines for management. Since organic farming and/or delayed cutting have significant landscape scale effects (in addition to their local effects), their location at landscape scale should be planned strategically to amplify the local effects of these AESs and other ones. Our results suggest that the scale at which their location should be planned is approximately 500 m from target fields to allow an effective network of favourable habitats that promotes resilience of carabid communities.

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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.2016.05.009>.

References

- Aviron, S., Burel, F., Baudry, J., Schermann, N., 2005a. Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agric. Ecosyst. Environ.* 108, 205–217. doi:<http://dx.doi.org/10.1016/j.agee.2005.02.004>.
- Aviron, S., Burel, F., Baudry, J., Schermann, N., 2005b. Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agric. Ecosyst. Environ.* 108, 205–217. doi:<http://dx.doi.org/10.1016/j.agee.2005.02.004>.
- Badenhausser, I., Mediene, S., Paris Le clerc, N., Bretagnolle, V., 2008. Effects of agri-environmental agreements on acridids and plant species richness in alfalfa crops. 22st International Symposium of the European Grassland Federation, Uppsala, Sweden.
- Bengtsson, J., Ahnström, J., Weibull, A.-C., 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *J. Appl. Ecol.* 42, 261–269. doi:<http://dx.doi.org/10.1111/j.1365-2664.2005.01005.x>.

- Bradbury, R.B., Allen, D.S., 2003. Evaluation of the impact of the pilot UK Arable Stewardship Scheme on breeding and wintering birds: few positive responses by birds were observed in the first two years of this new agri-environment scheme. *Bird Study* 50, 131–141.
- Bretagnolle, V., Gauffre, B., Meiss, H., et al., 2011. The Role of Grassland Areas within Grassland productivity and ecosystem services, 2011, 26, p. 251.
- Brodier, S., Aguiron, S., Cornulier, P., Bretagnolle, V., 2014. Local improvement of skylark and corn bunting population trends on intensive arable landscape: a case study of the conservation tool Natura 2000. *Anim. Conserv.* 17, 204–216.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Sci. Bus. Media.
- Cole, L.J., McCracken, D.L., Dennis, P., Downie, I.S., Griffin, A.L., Foster, G.N., Murphy, K.J., Waterhouse, T., 2002. Relationships between agricultural management and ecological groups of ground beetles (Coleoptera: Carabidae) on Scottish farmland. *Agric. Ecosyst. Environ.* 93, 323–336.
- Concepción, E.D., Díaz, M., Baquero, R.A., 2008. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. *Landsc. Ecol.* 23, 135–148. doi:http://dx.doi.org/10.1007/s10980-007-9150-2.
- Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tschamtkke, T., Verhulst, J., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management: landscape constrains the effectiveness of local management. *J. Appl. Ecol.* 49 doi:http://dx.doi.org/10.1111/j.1365-2664.2012.02131.x.
- Cressie, N., 1992. Statistics for spatial data. *Terra Nova* 4, 613–617.
- Di Giulio, M., Edwards, P.J., Meister, E., 2001. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *J. Appl. Ecol.* 38, 310–319.
- Eyre, M.D., Luff, M.L., Atlihan, R., Leifert, C., 2012. Ground beetle species (Carabidae, Coleoptera) activity and richness in relation to crop type, fertility management and crop protection in a farm management comparison trial: crop, fertility and crop protection effects on ground beetle activity. *Ann. Appl. Biol.* 161, 169–179. doi:http://dx.doi.org/10.1111/j.1744-7348.2012.00562.x.
- Fox, J., Weisberg, S., 2010. An R Companion to Applied Regression. Sage.
- Fuentes-Montemayor, E., Goulson, D., Park, K.J., 2011. The effectiveness of agri-environment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach: effects of agri-environment schemes on moths. *J. Appl. Ecol.* 48, 532–542. doi:http://dx.doi.org/10.1111/j.1365-2664.2010.01927.x.
- Garratt, M.P.D., Wright, D.J., Leather, S.R., 2011. The effects of farming system and fertilisers on pests and natural enemies: a synthesis of current research. *Agric. Ecosyst. Environ.* 141, 261–270.
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tschamtkke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic Appl. Ecol.* 11, 97–105. doi:http://dx.doi.org/10.1016/j.baee.2009.12.001.
- Gentleman, R., Ihaka, R., Bates, D., et al., 2009. The R project for statistical computing. URL <http://www.R-Project.org>.254.
- Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., 2010. Food security: the challenge of feeding 9 billion people. *Science* 327, 812–818. doi:http://dx.doi.org/10.1126/science.1185383.
- Hatten, T.D., Bosque-Pérez, N.A., Labonte, J.R., Guy, S.O., Eigenbrode, S.D., 2007. Effects of tillage on the activity density and biological diversity of carabid beetles in spring and winter crops. *Environ. Entomol.* 36, 356–368.
- Henckel, L., Börger, L., Meiss, H., Gaba, S., Bretagnolle, V., 2015. Organic fields sustain weed metacommunity dynamics in farmland landscapes. *Proc. R. Soc. Lond. B: Biol. Sci.* 282, 20150002.
- Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F., Niemelä, J., Rebane, M., et al., 2008. Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—a review. *Agric. Ecosyst. Environ.* 124, 60–71.
- Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V., Evans, A.D., 2005. Does organic farming benefit biodiversity? *Biol. Conserv.* 122, 113–130. doi: <http://dx.doi.org/10.1016/j.biocon.2004.07.018>.
- Hooper, D.U., Chapin Iii, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., et al., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3–35.
- Jeannel, R., 1941. Faune de France 39: Coléoptères Carabiques, Première Partie. Lechevalier, Paris.
- Judas, M., Dornieden, K., Strothmann, U., 2002. Distribution patterns of carabid beetle species at the landscape-level. *J. Biogeogr.* 29, 491–508.
- Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* 40, 947–969.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., Esteban, J., de Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., et al., 2006a. Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* 9, 243–254.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tschamtkke, T., Verhulst, J., West, T.M., Yela, J.L., 2006b. Mixed biodiversity benefits of agri-environment schemes in five European countries: biodiversity effects of European agri-environment schemes. *Ecol. Lett.* 9, 243–254. doi:http://dx.doi.org/10.1111/j.1461-0248.2005.00869.x.
- Kromp, B., 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.* 74, 187–228.
- Lang, A., 2000. The pitfalls of pitfalls: a comparison of pitfall trap catches and absolute density estimates of epigeal invertebrate predators in arable land. *Anz. Für Schädlingkunde J. Pest Sci.* 73, 99–106.
- Loreau, M., Naeem, S., Inchausti, P. (Eds.), 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford.
- Luff, M.L., 1975. Some features influencing the efficiency of pitfall traps. *Oecologia* 19, 345–357.
- Magura, T., Tóthmérész, B., Molnár, T., 2004. Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen. Hungary. *Landsc. Ecol.* 19, 747–759. doi:http://dx.doi.org/10.1007/s10980-005-1128-4.
- Maisonhaute, J.-É., Peres-Neto, P., Lucas, É., 2010a. Influence of agronomic practices, local environment and landscape structure on predatory beetle assemblage. *Agric. Ecosyst. Environ.* 139, 500–507. doi:http://dx.doi.org/10.1016/j.agee.2010.09.008.
- Maisonhaute, J.-É., Peres-Neto, P., Lucas, É., 2010b. Influence of agronomic practices, local environment and landscape structure on predatory beetle assemblage. *Agric. Ecosyst. Environ.* 139, 500–507.
- Melnichuk, N.A., Olfert, O., Youngs, B., Gillott, C., 2003. Abundance and diversity of Carabidae (Coleoptera) in different farming systems. *Agric. Ecosyst. Environ.* 95, 69–72.
- Menalled, F.D., Lee, J.C., Landis, D.A., 1999. Manipulating carabid beetle abundance alters prey removal rates in corn fields. *BioControl* 43, 441–456.
- Myers, J.A., Harms, K.E., 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecol. Lett.* 12, 1250–1260.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., Suggests, M., 2007. The vegan package. *Community Ecol. Package* 631–637.
- Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., et al., 2014. EU agricultural reform fails on biodiversity. *Science* 344, 1090–1092.
- Peach, W.J., Lovett, L.J., Wotton, S.R., Jeffs, C., 2001. Countryside stewardship delivers cirl buntings (*Emberiza cirius*) in Devon, UK. *Biol. Conserv.* 101, 361–373.
- Perkins, A.J., Maggs, H.E., Watson, A., Wilson, J.D., 2011. Adaptive management and targeting of agri-environment schemes does benefit biodiversity: a case study of the corn bunting *Emberiza calandra*. *J. Appl. Ecol.* 48, 514–522.
- Piñeiro, G., Perelman, S., Guerschman, J.P., Paruelo, J.M., 2008. How to evaluate models: observed vs. predicted or predicted vs. observed? *Ecol. Model.* 216, 316–322. doi:http://dx.doi.org/10.1016/j.ecolmodel.2008.05.006.
- Puech, C., Poggi, S., Baudry, J., Aviron, S., 2014. Farming practices affect natural enemies at the landscape scale? *Landscape Ecol.* 30, 125–140. doi:http://dx.doi.org/10.1007/s10980-014-0103-2.
- Purtauf, T., Dauber, J., Wolters, V., 2005. The response of carabids to landscape simplification differs between trophic groups. *Oecologia* 142, 458–464. doi: <http://dx.doi.org/10.1007/s00442-004-1740-y>.
- Quantum GIS, 2013. Development Team, 2012. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Free Softw. Found. India.
- Ricci, B., Franck, P., Toubon, J.-F., Bouvier, J.-C., Sauphanor, B., Lavigne, C., 2009. The influence of landscape on insect pest dynamics: a case study in southeastern France. *Landscape Ecol.* 24, 337–349. doi:http://dx.doi.org/10.1007/s10980-008-9308-6.
- Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* 39, 157–176. doi:http://dx.doi.org/10.1046/j.1365-2664.2002.00695.x.
- Schweiger, O., Maelfait, J.-P., van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., et al., 2005. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *J. Appl. Ecol.* 42, 1129–1139.
- Smith, H.G., Dänhardt, J., Lindström, A.A., Rundlöf, M., 2010. Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. *Oecologia* 162, 1071–1079.
- Sokal, R.R., Rohlf, F.J., 1995. Biometry: the principles and practice of statistics in biological research. WH Freeman Co., San Francisco. *Sokal Biometry Princ. Pract. Stat. Biol. Res.*
- Thiele, H.-U., et al., 1977. Carabid beetles in their environments. A Study on Habitat Selection by Adaptation in Physiology and Behaviour. Springer-Verlag.
- Thomas, C.F.G., Brown, N.J., Kendall, D.A., 2006. Carabid movement and vegetation density: Implications for interpreting pitfall trap data from split-field trials. *Agric. Ecosyst. Environ.* 113, 51–61. doi:http://dx.doi.org/10.1016/j.agee.2005.08.033.
- Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. *Nature* 418, 671–677.
- Tilman, D., 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77, 350. doi:http://dx.doi.org/10.2307/2265614.
- Tschamtkke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol. Lett.* 8, 857–874. doi:http://dx.doi.org/10.1111/j.1461-0248.2005.00782.x.
- Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: a

- hierarchical meta-analysis. *J. Appl. Ecol.* 51, 746–755. doi:<http://dx.doi.org/10.1111/1365-2664.12219>.
- Vickery, J.A., Bradbury, R.B., Henderson, I.G., Eaton, M.A., Grice, P.V., 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biol. Conserv.* 119, 19–39.
- Weibull, A.-C., Östman, Ö., Granqvist, Å., 2003a. Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodivers. Conserv.* 12, 1335–1355.
- Weibull, A.-C., Östman, Ö., Granqvist, Å., 2003b. Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodivers. Conserv.* 12, 1335–1355.
- Whittingham, M.J., 2007. Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *J. Appl. Ecol.* 44, 1–5.
- Whittingham, M.J., 2011. The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? *J. Appl. Ecol.* 48, 509–513.
- Woodcock, B.A., Savage, J., Bullock, J.M., Nowakowski, M., Orr, R., Tallwin, J.R.B., Pywell, R.F., 2014. Enhancing floral resources for pollinators in productive agricultural grasslands. *Biol. Conserv.* 171, 44–51. doi:<http://dx.doi.org/10.1016/j.biocon.2014.01.023>.

Further reading

- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182–188. doi:[10.1016/S0169-5347\(03\)00011-9](http://dx.doi.org/10.1016/S0169-5347(03)00011-9).
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., others, 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B Biol. Sci.* 268, 25–29.
- Herzog, F., Dreier, S., Hofer, G., Marfurt, C., Schüpbach, B., Spiess, M., Walter, T., 2005. Effect of ecological compensation areas on floristic and breeding bird diversity in Swiss agricultural landscapes. *Agric. Ecosyst. Environ.* 108, 189–204.