

Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis

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Agri-environmental management (AEM) is heralded as being key to biodiversity conservation on farmland, yet results of these schemes have been mixed, making their general utility questionable. We test with meta-analysis whether the benefits of AEM for species richness and abundance of plants and animals are determined by the surrounding landscape context. Across all studies (109 observations for species richness and 114 observations for abundance), AEM significantly increased species richness and their abundance. More specifically, we test the hypothesis that AEM benefits species richness and abundance (i.e. increases the difference between fields with and without AEM) more in simple than in complex landscapes. In croplands, species richness but not abundance was significantly enhanced in simple but not in complex landscapes. In grasslands, AEM effectively enhanced species richness and abundance regardless of landscape context. Pollinators were significantly enhanced by AEM in simple but not in complex landscapes in both croplands and grasslands. Our results highlight that the one-size-fits-all approach of many agri-environmental programmes is not an efficient way of spending the limited funds available for biodiversity conservation on farmland. Therefore, we conclude that AEM should be adapted to landscape structure and the species groups at which they are targeted.

Keywords: agri-environment schemes; complex landscape; cropland; grassland; organic farming; simple landscape

1. INTRODUCTION

Biodiversity conservation cannot rely on protected areas alone, as sustainable conservation requires strategies for managing whole landscapes including areas allocated mainly to production [1]. More than half of the Earth's terrestrial surface is moulded by agriculture, so the contribution of agricultural areas to biodiversity is critical for successful long-term conservation [2]. Ecologists and conservation practitioners often view agricultural land as a biological desert or a hostile matrix isolating habitat fragments. However, agroecosystems may also provide environmental benefits and important ecosystem services, such as pollination and biological control [3,4]. High diversity may not necessarily be critical for maintaining ecosystem processes under constant environmental conditions, but might become important under environmental change [5,6]. Maintaining this insurance in agricultural landscapes requires a minimum of natural habitat to provide a sufficient species pool [7].

Conservation of biodiversity needs a landscape perspective, combining conservation in nature reserves with that on farmland in a well-balanced way [8]. Nature conservation on farmland is generally implemented through

agri-environment schemes (AES) or equivalent schemes outside Europe (e.g. the Environmental Quality Incentives Programme of the USDA), which have been initiated in many countries to compensate farmers for any loss of income associated with measures to enhance environmental benefits [9]. Local impact reduction of farming practices (often subsidized in AES) may enhance biodiversity (e.g. [10–13]), but offers no guarantee for success [9,14]. In a quantitative synthesis, Bengtsson *et al.* [15] found that organic farming had generally positive (local) effects on biodiversity, but these effects differed between species groups and spatial scales. Attwood *et al.* [16] reviewed local management effects on arthropods and found arthropod richness to be significantly higher in areas of less intensive land use. Though the importance of habitat heterogeneity in farmland biodiversity has been emphasized [10], no quantitative synthesis has been carried out to analyse the relative effects of local and landscape scale management on farmland biodiversity. In their review, Tschardt *et al.* [8] suggested that agri-environmental management (AEM) may be effective in increasing species richness in simple, but not in complex landscapes, because farms in complex landscapes are likely to already have high diversity. By contrast, Duelli & Obrist [17] concluded that AEM has a much greater chance of success in regions where source populations survive in nearby natural or semi-natural habitats. Similarly, Kleijn & Sutherland [9] suggested

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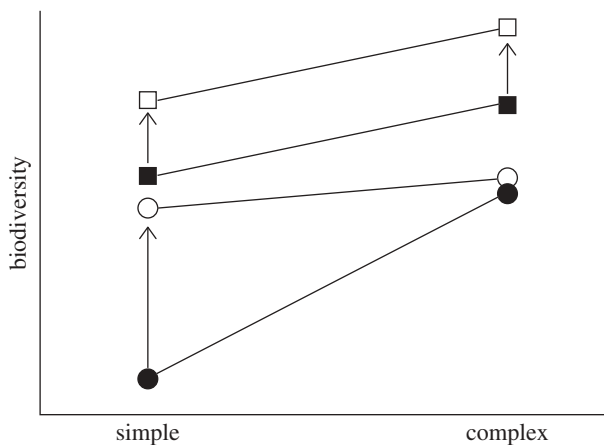


Figure 1. Hypothesized relationship between biodiversity (species richness) and local management in dependence of the structural composition of agricultural landscapes. AEM is contrasted against conventional management. Landscape type is classified as simple (0–20% cover of semi-natural habitat) and complex (>20% semi-natural habitat; see [34,35]). The large black arrows indicate benefits of biodiversity, when changing from conventional management to AEM. Open boxes, grassland with AEM; filled boxes, grassland without AEM; open circles, cropland with AEM; filled circles, cropland without AEM.

that AEM may have much more pronounced effects in extensively farmed landscapes than in intensively farmed landscapes. To address this controversy, we test the following two hypotheses using a meta-analysis.

Hypothesis 1: The benefits of AEM in terms of enhanced species richness and abundance of a variety of organism groups are smaller in complex landscapes (with a high proportion of semi-natural habitats) than in simple landscapes (with a low proportion of semi-natural habitats).

Hypothesis 2: Since the effectiveness of agroecosystem diversification to enhance biological control is known to differ with farmland type [18], we test the hypothesis that AEM has a larger effect in croplands than in grasslands. Grasslands are generally less disturbed by agricultural activities than croplands and generally support higher biodiversity [18], so they can be expected to support more species and individuals and to be less affected by the surrounding landscape and short-term AEM (figure 1).

Accordingly, the effectiveness of AEM (biodiversity difference between AEM and control fields) in croplands should be highest in simple landscapes and lowest in complex landscapes, whereas in grasslands, a positive effect of AEM can be expected in both landscape types (figure 1).

2. MATERIAL AND METHODS

We tested our research hypotheses using a meta-analysis. In ecology, there is a growing need for quantitative research synthesis to generate higher order conclusions [19,20]. In contrast to qualitative and descriptive traditional reviews, meta-analysis allows the quantitative analysis and summary of the results of several independent studies examining the same question [21–25]. In meta-analysis, the magnitude of effects (effect size) is quantified from each individual study, and these are then used to calculate the combined

(overall) magnitude and significance of the effect under the meta-analytical study [21]. Therefore, meta-analysis is an appropriate method for examining the general evidence for or against a specific hypothesis [15].

(a) Data collection and criteria for inclusion

We conducted a systematic literature survey using keyword searches in the ISI Web of Science database (until July 2008) and by searching the reference lists of previous syntheses on related topics [9,12,15,16]. The combinations of the following keywords were used: agri*, biodiversity, farming, integrated, intensity, management, organic and species. We included only those studies, which fulfilled the following criteria: (i) studies that compared the species richness (Shannon diversity in case of Genghini *et al.* [26]) and/or the abundance of terrestrial taxa (invertebrates, vertebrates and plants) between farming systems managed at different intensity levels (hereafter, intensive versus extensive agricultural systems; for detailed classification see §2b). Set-aside studies were excluded, because set-aside is usually not an actively managed farming system [27]; (ii) studies that were carried out at the landscape scale and included at least two separate fields in each category, i.e. in intensive and extensive agricultural systems (field-scale studies were excluded); and (iii) studies that reported means, standard deviations (s.d.), standard errors of means (s.e.m.) or confidence intervals (CI) and sample sizes for both management systems. As the figures in Rundlöf & Smith [28] and Rundlöf *et al.* [29,30] were not produced on the same scale that was used in their analyses, estimates of means and standard errors were obtained from the authors. Observations of multiple taxa and/or of different geographical regions per individual studies were included separately in the dataset and considered independently. This may not strictly meet the assumption of meta-analysis that each observation is independent of all others [23,31], but it allowed us to more fully explore the effects of landscape composition on the studied systems [22,32]. If a paper reported more than two management intensity levels or several survey periods, we selected the two management systems with the highest contrast in land-use intensity and the most recent survey. We used unpublished means and standard deviations of Kleijn *et al.* [14] to include observations from this study and included unpublished data from a recent study by the first author to increase the sample size (see P. Batáry, A. Báldi, D. Kleijn & T. Tscharrntke 2010, unpublished data in electronic supplementary material, tables S1 and S2) and the statistical power of the analyses.

Altogether, we found 109 observations of 47 case studies for species richness (electronic supplementary material, table S1) and 114 observations of 46 case studies for abundance (electronic supplementary material, table S2). The majority of the studies compared conventional with organic management (about 75% of all observations in both datasets), and the latter was often part of AES. Hereafter, we refer to these local extensification of farming practices as AEM. AEM includes environmentally friendly agricultural practices on the field or farm level, such as reductions in agrochemical input, soil cultivation, mowing frequency or cattle density, as well as enhancement of organic farming or field margin strip cultivation. In Europe (European studies dominate our datasets; approx. 80% of observations), many of these practices are facilitated by national and European Union subsidies [9,33].

(b) Classifications based on landscape composition and farming system

To test the dependence of the effect of AEM on landscape context we classified studies as having been carried out in simple or complex landscapes. Landscapes with high proportions of semi-natural grasslands, forests, hedgerows, tree lines or wetlands (i.e. semi-natural areas) were referred to as 'complex' (>20% cover of semi-natural habitat), while landscapes with few of these habitats as 'simple' (0–20% semi-natural habitat). The 20 per cent threshold was based on earlier studies [34–36]. In addition to simple and complex landscapes, Tschardt *et al.* [8] distinguished cleared landscapes (<1% non-crop habitat). However, very few studies had been conducted in cleared landscapes (see electronic supplementary material, tables S1 and S2). We, therefore, included studies from landscapes with less than 1 per cent non-crop habitat in the simple landscape category. No analysis was possible using semi-natural area per cent as a continuous variable (i.e. continuous meta regression), because relatively few studies provided exact geographical codes for all study fields, and the distribution of the proportion of semi-natural area of these studies was unbalanced.

We used the landscape data provided in the papers and checked the study areas using the software GOOGLE EARTH [37]. The categorization was done independently by two authors (P.B. and A.B.). For a subset of studies, for which CORINE Land Cover 2000 datasets (hereafter, CLC 2000; [38]) and the exact location of study sites (Geographical Information System coordinates, accurate maps or settlement designations) were available, we measured the total proportion of semi-natural areas (within a radius of 1000 m of the locations) with ARCGIS 9.2 [39]. CORINE (Coordination of Information on the Environment) is a programme developed by the European Environment Agency, which has generated Europe-wide environmental data, including land-cover data. CLC 2000 data are available for 26 European countries and distinguish 44 land cover (or habitat) categories. The 17 categories starting with CLC 2000 codes three or four indicate semi-natural habitats and were used to calculate the proportion of these within a radius of 1000 m.

The species richness and abundance datasets were divided into two main parts according to the investigated land-use following Rounsevell *et al.* [40]: croplands (arable and permanent crops for food) versus grasslands. Croplands mainly consisted of cereal fields, but a small number consisted of vineyards, orchards, olive groves, cotton fields, cacao, coffee agroforestry and vegetable fields (share of permanent crop observations in species richness and abundance datasets: 11 and 15%). Grasslands were permanent agroecosystems for grazing or hay making, but also included a few studies performed on field boundaries or ditch banks (share of field boundary or ditch bank observations in species richness and abundance datasets: 11 and 9%).

(c) Effect size calculation

We used Hedges' *d* as an estimate of the standardized mean difference (i.e. the effect size). It expresses the strength of an effect in multiples of the studies standard deviation, i.e. by how much the effect is increased above the noise level. A value of 1 indicates that the treatment group was 1 s.d. above the value of the control group. Hedges' *d* has the advantage that it is not biased by small sample size [21]. Effect sizes and their non-parametric estimates of variance

were calculated for all observations based on the mean, standard deviation and sample size (number of studied fields) of species richness and abundance of intensively (control) and extensively (AEM) used agroecosystems [21]. Effect size was positive if species richness or abundance was higher in the extensive than in the intensive fields. Non-parametric variance estimates use only the sample sizes from the experimental and control groups rather than incorporating the effect size into the calculation [41]. This alternative estimate makes few assumptions and may be less constrained by the assumptions of large sample theory [21].

(d) Meta-analyses

Categorical meta-analysis was performed separately for species richness and abundance in croplands and grasslands. The categorical factor was based on the landscape complexity, i.e. simple or complex landscape. We used random effects models (effect sizes nested within studies) with resampling (4999 iterations) to calculate the grand mean effect size for each analysis, which allowed effect size estimates to vary not only owing to sampling error, but also owing to biological or environmental differences between organisms and studies [24,32,42]. The output of each statistical test consisted of the mean effect size for the analysis with an accompanying bias-corrected bootstrapped 95% CI [41] and a total heterogeneity statistic (*Q*). The heterogeneity statistic is a weighted sum of squares and is tested against a χ^2 distribution with $n - 1$ d.f. [32]. Estimates of the effect size were considered to be significantly different from zero if their 95% CI did not include zero [43].

The total heterogeneity in categorical meta-analysis—similar to the partitioning of variance in analysis of variance—can be partitioned into variance explained by the categorical factor in the model (between-group heterogeneity) and residual error variance (within-group heterogeneity) with χ^2 -tests indicating their significance [41,42]. Significant between-group heterogeneity indicated support that species richness or abundance responses to AEM differed in different landscape types [24]. We considered a significant mean effect size in simple landscapes but not in complex landscapes and an additional significant between-group heterogeneity as support for the hypothesis (H1) that AEM is more effective in simple than in complex landscapes (figure 1). To test our second hypothesis (H2) that AEM has a larger effect in croplands than grasslands of simple landscapes, we performed meta-analyses on species richness and abundance. In these analyses all observations were included, and the categorical factor was habitat type, i.e. cropland versus grassland. Here we have to note that it was not possible to test for an interaction landscape type (simple versus complex) and agricultural system (croplands versus grasslands) with our meta-analysis software (METAWIN 2.0; [42]).

Studies included in the analysis examined the response of many different species groups, allowing us to analyse the response of different taxonomic or functional groups separately (electronic supplementary material, tables S1 and S2). This was only done for species groups for which three or more observations were available. Arthropods were further categorized in functional groups (herbivores, pollinators), but no such comparison was possible for predatory arthropods, because of data deficiency in either of the two categories (simple or complex). Within- and between-group heterogeneities were tested with χ^2 -tests.

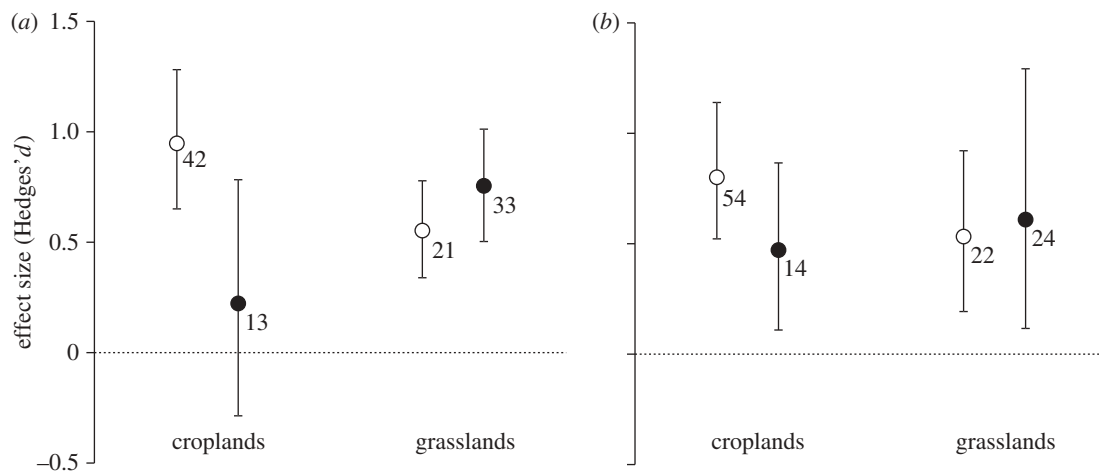


Figure 2. The effects of AEM on (a) species richness and (b) abundance depending on landscape type (simple versus complex) and agricultural system (croplands versus grasslands). Indicated is mean effect size \pm 95% CI. The mean effect size is significantly different from zero, if the CIs do not overlap with zero [42]. Numbers indicate sample sizes. Open circles, simple; filled circles, complex.

(e) Publication bias

Studies finding a significant effect are more likely to be published than studies finding no effects. This ‘file-drawer’ phenomenon [44–46] may bias the outcome of meta-analyses. We, therefore, examined publication bias using Rosenthal’s technique of a fail-safe number, which calculates the number of non-significant, unpublished studies that need to be added to a summary analysis in order to change the results from significant into non-significant. Thus, the higher the fail-safe number, the more credibility a significant result has [31]. More precisely, a fail-safe number is often considered robust if it is greater than $5n + 10$, where n is the original number of studies [47]. However, we have to note that random-effects model fail-safe numbers are usually quite a bit smaller than their fixed-effects model equivalents [46]. Furthermore, there was a geographical bias in our dataset, whereby most studies originated from Europe and the temperate zone (like in the earlier syntheses [12,15]). This bias is probably owing to the many more studies performed in Europe than in other continents, which compared the biodiversity of AEM and control fields at landscape level and also fulfilled our study selection criteria. All meta-analyses were performed with METAWIN 2.0 software [42].

3. RESULTS

(a) Hypothesis 1: AEM has stronger effects in simple than in complex landscapes

In croplands, the standardized average effect size for observations of species richness in simple but not in complex landscapes was significantly greater than zero (figure 2). In other words, AEM had a positive effect on species diversity in simple but not complex landscapes. This contrast was further supported by a significant between-group heterogeneity (table 1). The average effect sizes of the abundance data differed significantly from zero in both landscape types (figure 2b). Sample sizes were larger for simple than for complex landscapes in croplands (figure 2), however, this did not appear to affect the results as the 95% CIs were similar in size and overlapped considerably (table 1). In grasslands, AEM resulted in significantly higher species richness

Table 1. Heterogeneity statistics and Rosenthal’s fail-safe numbers for each model of figure 2 analysing the effect of landscape type (simple versus complex) on agricultural intensification (measured as effect size, see §2) in croplands versus grasslands. (Between- (Q_B) and within-group (Q_W) heterogeneities were tested with a χ^2 -test. n , number of individual comparisons.)

	n	Q_B	$p(Q_B)$	Q_W	$p(Q_W)$	fail-safe
croplands						
species richness	55	4.22	0.040	51.09	0.549	527
abundance	68	0.96	0.328	66.98	0.443	723
grasslands						
species richness	54	1.19	0.276	53.02	0.434	1100
abundance	46	0.04	0.840	39.64	0.659	113

and abundance regardless of landscape type (figure 2). Overall, the within-group heterogeneities of the four above categorical meta-analyses were non-significant (table 1). Rosenthal’s fail-safe numbers were robust for all categorical meta-analyses with exception of abundance analysis in grasslands (table 1). Here we note that in the latter case (abundance analysis in grasslands based on 46 observations) it is difficult to consider a fail-safe number requiring more than 110 missing studies unrobust.

(b) Hypothesis 2: AEM has a larger effect in cropland than grassland

Regarding our second hypothesis (H2), we found no significant evidence that AEM had a larger effect in croplands than in grasslands. AEM effects were positive for both species richness (between-group heterogeneity: $Q_B = 2.294$, $p = 0.130$; mean effect sizes and lower–upper CIs for cropland and grassland: 0.93, 0.63–1.27, and 0.58, 0.36–0.80) and abundance ($Q_B = 1.135$, $p = 0.287$; mean effect sizes and lower–upper CIs for cropland and grassland: 0.79, 0.52–1.15, and 0.51, 0.21–0.86) regardless of land-use types (cropland versus grassland).

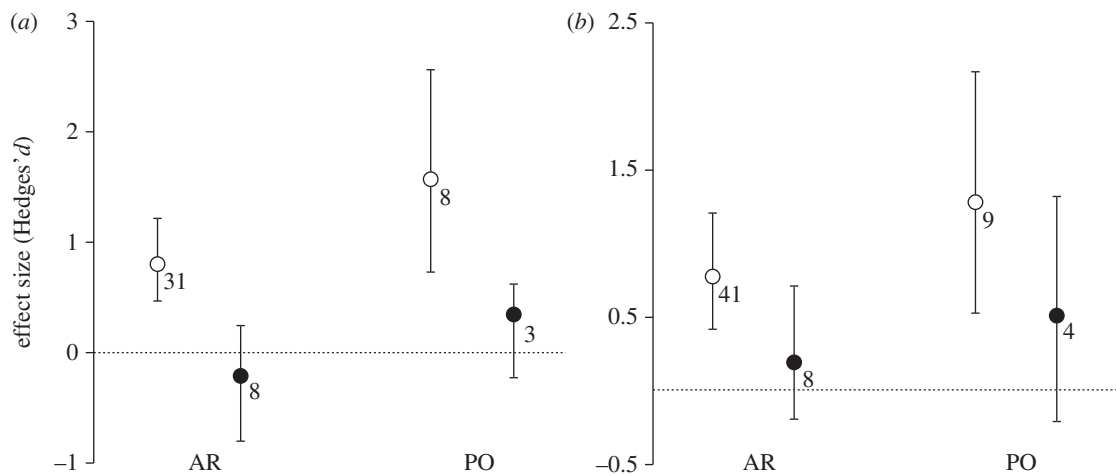


Figure 3. The effects of AEM in croplands on (a) species richness and (b) abundance of all arthropods (AR) and pollinators (PO) depending on landscape type (simple versus complex). The mean and 95% CI is shown for each analysis. Numbers indicate sample sizes. Open circles, simple; filled circles, complex.

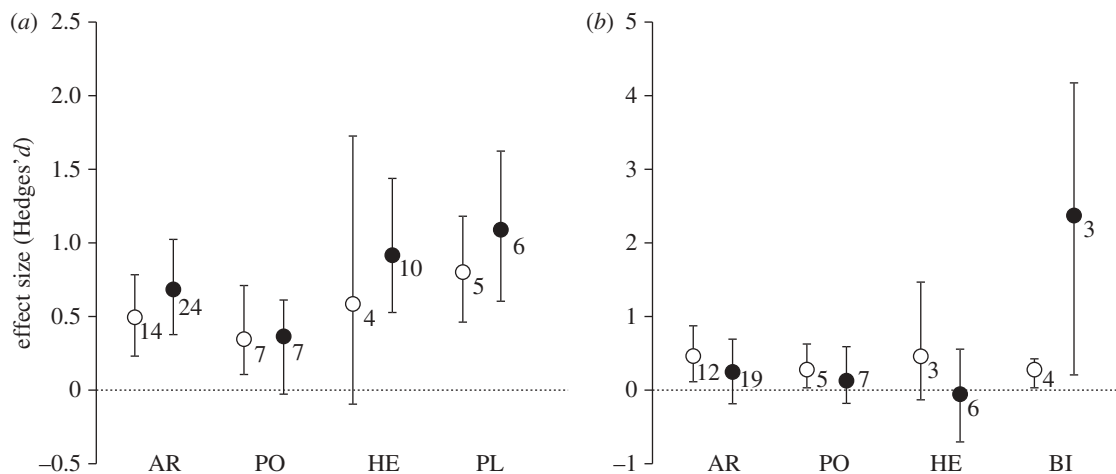


Figure 4. The effects of AEM in grasslands on (a) species richness and (b) abundance of all arthropods (AR), pollinators (PO), herbivores (HE), plants (PL) and birds (BI) depending on landscape type (simple versus complex). The mean and 95% CI is shown for each analysis. Numbers indicate sample sizes. Open circles, simple; filled circles, complex.

(c) Different taxonomic and functional groups show different responses to AEM in simple versus complex landscapes

In croplands, pooling of all observations of arthropods was necessary to have sufficient replicates for analysis. The effect sizes of species richness and abundance of all arthropods were significantly greater than zero in simple, but not in complex landscapes (figure 3*a,b*). However, we found significant between-group heterogeneity only in the case of all arthropod richness (electronic supplementary material, table S3). Observations on pollinators were available in sufficient number to merit separate analyses. For this functional group, AEM was effective in simple, but not in complex landscapes (figure 3*a,b*).

In grasslands, we analysed effect sizes of the species richness of plants, all arthropods, pollinators and herbivores as well as effect sizes of the abundance of all arthropods, pollinators, herbivores and birds (figure 4*a,b*; electronic supplementary material, table S3). AEM had significant positive effects on the species richness of plants and all arthropods in both landscape types and on pollinators' species richness in simple

landscapes only (figure 4*a*). Similar to the effects in croplands, AEM in grasslands had contrasting effects on arthropod and pollinator abundances in simple and complex landscapes, but between-group heterogeneity remained non-significant. Bird abundances were significantly positively affected by AEM in the two landscape types, but herbivore abundances were not. However, the low fail-safe numbers of the two latter analyses suggest publication bias, thus questioning the strength of these results (electronic supplementary material, table S3).

4. DISCUSSION

The impact of landscape context on the effectiveness of AEM that reduces management intensity on agricultural fields seems to differ between farming system and species group. In cropland, AEM was more effective in enhancing species richness in simple than in complex landscapes. Furthermore, pollinators and all arthropods combined consistently showed more positive responses to AEM in croplands embedded in simple than in complex landscapes. By contrast, AEM in grasslands was equally effective in complex and simple landscapes, with positive

effects on plants and birds, independent of landscape complexity; only pollinator richness and abundance of all arthropods combined responded to landscape context in cropland and grassland in a similar way. According to this meta-analysis, the hypothesis (H1) raised originally by Tscharntke *et al.* [8] that AEM is more effective in terms of species richness in simple than in complex landscapes seems to apply only for cropland, and not for grassland, which is usually less intensively managed. In addition, in grasslands taxon-specific differences can be important, and management options may depend on the specific group requiring conservation. Finally, regarding our second hypothesis (H2), we found no evidence that AEM had a larger effect in croplands than in grasslands.

We found that landscape context moderates effects of AEM on species richness in croplands but not in grasslands. One might argue that arthropods, which tend to be more affected by landscape complexity (figures 3 and 4) made up a larger proportion of the studied species groups in croplands than in grasslands. However, arthropods were the investigated species group in about 70 per cent of all studies (electronic supplementary material, table S1) making it unlikely that a different representation of species groups explains the observed difference in response between the two farming systems. Another explanation may be that studies in grasslands have been carried out in less intensively farmed landscapes than studies in croplands. Only a few studies synthesized in our meta-analyses reported the amount of fertilizer use in grasslands and croplands (a commonly used indicator of land-use intensity; [33]), which did not allow statistical analysis. However, croplands seem to receive roughly twice as much nitrogen fertilizer as grasslands. The most intriguing difference is the complete removal of the vegetation in arable systems, so spillover from semi-natural landscape elements to agricultural fields may be much more important than in grasslands [48–50]. Grasslands were all perennial agroecosystems (with few exceptions, which were studies on field boundaries and ditch banks) that have a more stable plant and animal community [51], which hampers the establishment of invading plant and animal species from the surrounding landscape-wide species pool.

Across farmland types and for both abundance and species richness, pollinating arthropods were the only species group for which the effect sizes were consistently significant in simple and non-significant in complex landscapes indicative of landscape-mediated effectiveness of AEM (although between-group heterogeneities were not significant, possibly because of lower sample sizes at this level of analysis [43]). Except for very extensively managed agricultural areas, major pollinator groups such as bees or hover flies nest or hibernates in semi-natural habitats and exploit agricultural fields mainly for foraging [52,53]. Probably as a result, pollinator richness and the pollination services they provide, decline exponentially with increasing distance from natural or semi-natural habitats such as field margins, species-rich grasslands or forests [54–56]. In complex landscapes, where most fields are located at short distances from semi-natural habitats, the continuous spillover of pollinators from semi-natural habitats to agricultural fields may obscure differences caused by local management [30]. The

complexity of the landscape in the direct vicinity (<1 km) of the treatment fields corresponds well with the mobility of pollinators [57], while plant populations may be sedentary or benefit from seed rain, and bird species also greatly differ in mobility. Other species groups are often less strongly related to semi-natural habitats [17]. Many herbivorous arthropod species can hibernate in agricultural fields and do not need to colonize the fields from semi-natural habitats each spring, while others are colonizers. Arable or grassland plant species survive year round in agricultural fields either as perennial plants or as seeds or buds, but can also be influenced by landscape context [58–60]. The high mobility of birds allows many species to locate and exploit fields of high resource quality, independent of landscape complexity [61].

We found no evidence for AEM having larger effects on species richness or abundance in croplands than in grasslands. This supports findings of Kleijn *et al.* [33], who found a similarly declining relationship between land-use intensity and plant species richness in grasslands and croplands. This suggests that schemes reducing the intensity of farming will have a similar impact in grasslands and croplands. The mechanism may lie in the fact that the disturbance regime in intensively managed grasslands is very high and is probably not very dissimilar from that in intensively managed arable fields. Agrochemical input for weed and pest control is low in extensively managed crops reducing the disturbance regime and resembling annually cut or grazed grasslands.

Although the geographical coverage of this study is somewhat better than previous reviews on related topics (e.g. [9,12,15]), it is still subject to considerable geographical bias. Most of the observations that were used in this study (*ca* 80% for both species richness and abundance datasets) came from Europe and only few from the Americas. Africa and Australia were not included at all, while Asia was represented by studies from Indonesia alone. However, within Europe geographical coverage was fairly good, with observations from 12 to 14 countries for species richness and abundance analyses. Results should be interpreted bearing this geographical bias in mind [27].

Bengtsson *et al.* [15] argued in their meta-analysis that it would be desirable to take the sampling design into account. In our study quite a lot of observations used a matched paired study design (AEM fields paired with control fields). These paired observations were though very unbalanced within landscape types (simple versus complex) and farming systems (cropland versus grassland), which did not allow us to perform robust meta-analyses on solely paired design observations. We agree with Bengtsson *et al.* [15] that in case of matched pair studies there is a risk of producing a reduced difference between the farming practices. When conventional and organic fields are compared, without pair design, differences between the systems can, in most cases, be attributed to landscape simplification rather than farming system.

5. CONCLUSIONS

This study shows that, when average effects of many studies are considered, AEM effectively enhances

abundance in croplands, and species richness and abundance in grasslands regardless of landscape context. In addition, landscape complexity is moderating effects of AEM, contingent on farming system, and taxonomic and functional group. In agricultural grasslands and for species groups such as plants and birds, AEM is equally effective in complex and simple landscapes, while structurally complex landscapes generally support higher biodiversity levels than simple landscapes [8,62]. By contrast, in croplands and for arthropods, AEM is more effective in simple than in complex landscapes. The high effectiveness of AEM in enhancing arthropods of croplands is particularly important because of the associated ecosystem services such as pollination and pest control [63,64]. Our results clearly indicate that AEM in croplands should preferentially be implemented in structurally simple landscapes, because only in these can local AEM significantly and efficiently enhance agroecosystem functioning and services. This can be done by increasing the proportion of semi-natural habitats, or by reducing agrochemical input [65,66]. However, our study did not address effects on absolute species numbers. Meta-analyses only consider relative effects between AEM and conventional agriculture. Because different studies use different sampling designs, across-study comparisons of species richness in simple and complex landscapes are meaningless. Other studies, however, suggest that complex agricultural landscapes with their high amount of semi-natural areas generally have much larger species pools than simple landscapes and are inhabited by more endangered species [33,67]. For this reason alone it is important to preserve these landscapes [68]. Our results suggest that in complex grassland landscapes AEM may help preserve farmland biodiversity but in complex croplands it is not a very effective tool for this purpose. This study highlights that the one-size-fits-all approach of many agri-environmental programmes [9] is not a very efficient way of spending the limited funds available for biodiversity conservation on farmland. The design of agri-environmental programmes should be targeted to the nature of the landscapes of the regions in which they are implemented [69] and the type of species groups at which they are targeted.

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REFERENCES

- Margules, C. R. & Pressey, R. L. 2000 Systematic conservation planning. *Nature* **405**, 243–253. (doi:10.1038/35012251)
- Tallis, H., Goldmann, R., Uhl, M. & Brosi, B. 2009 Integrating conservation and development in the field: implementing ecosystem service projects. *Front. Ecol. Environ.* **7**, 12–20. (doi:10.1890/080012)
- Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. & Tscharntke, T. 2007 Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* **274**, 303–313. (doi:10.1098/rspb.2006.3721)
- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., Tylianakis, J. M., Van Nouhuys, S. & Vidal, S. 2007 Conservation biological control and enemy diversity on a landscape scale. *Biol. Cont.* **43**, 294–309. (doi:10.1016/j.biocontrol.2007.08.006)
- Yachi, S. & Loreau, M. 1999 Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. USA* **96**, 1463–1468. (doi:10.1073/pnas.96.4.1463)
- Loreau, M., Mouquet, N. & Gonzalez, A. 2003 Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl Acad. Sci. USA* **100**, 12 765–12 770. (doi:10.1073/pnas.2235465100)
- Landis, D. A. & Marino, P. C. 1999 Landscape structure and extra-field processes: impact on management of pests and beneficials. In *Handbook of pest management* (ed. J. R. Ruberson), pp. 79–104. New York, NY: Marcel Dekker Inc.
- Tscharntke, 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:10.1111/j.1461-0248.2005.00782.x)
- Kleijn, D. & Sutherland, W. J. 2003 How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* **40**, 947–969. (doi:10.1111/j.1365-2664.2003.00868.x)
- 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)
- Primdahl, J., Peco, B., Schramek, J., Andersen, E. & Oñate, J. J. 2003 Environmental effects of agri-environmental schemes in Western Europe. *J. Environ. Manag.* **67**, 129–138. (doi:10.1016/S0301-4797(02)00192-5)
- 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:10.1016/j.biocon.2004.07.018)
- Letourneau, D. K. & Bothwell, S. G. 2008 Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional. *Front. Ecol. Environ.* **6**, 430–438. (doi:10.1890/070081)
- Kleijn, D. *et al.* 2006 Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* **9**, 243–254. (doi:10.1111/j.1461-0248.2005.00869.x)
- Bengtsson, J., Ahnström, J. & Weibull, C. 2005 The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *J. Appl. Ecol.* **42**, 261–269. (doi:10.1111/j.1365-2664.2005.01005.x)
- Attwood, S. J., Maron, M., House, A. P. N. & Zammit, C. 2008 Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? *Global Ecol. Biogeogr.* **17**, 585–599. (doi:10.1111/j.1466-8238.2008.00399.x)
- Duelli, P. & Obrist, M. K. 2003 Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat. *Basic Appl. Ecol.* **4**, 129–138. (doi:10.1078/1439-1791-00140)
- Andow, D. A. 1991 Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* **36**, 561–568. (doi:10.1146/annurev.en.36.010191.003021)
- Gurevitch, J., Curtis, P. S. & Jones, M. H. 2001 Meta-analysis in ecology. *Adv. Ecol. Res.* **32**, 199–247. (doi:10.1016/S0065-2504(01)32013-5)
- Stewart, G. 2010 Meta-analysis in applied ecology. *Biol. Lett.* **6**, 78–81. (doi:10.1098/rsbl.2009.0546)

- 21 Hedges, L. V. & Olkin, I. 1985 *Statistical methods for meta-analysis*. San Diego, CA: Academic Press.
- 22 Gurevitch, J., Morrow, L. L., Wallace, A. & Walsh, J. S. 1992 A meta-analysis of competition in field experiments. *Am. Nat.* **140**, 539–572. (doi:10.1086/285428)
- 23 Arnqvist, G. & Wooster, D. 1995 Meta-analysis: synthesizing research findings in ecology and evolution. *Trends Ecol. Evol.* **10**, 236–240. (doi:10.1016/S0169-5347(00)89073-4)
- 24 Gurevitch, J. & Hedges, L. V. 1999 Statistical issues in ecological meta-analyses. *Ecology* **80**, 1142–1149. (doi:10.1890/0012-9658(1999)080[1142:SIEMA]2.0.CO;2)
- 25 Cooper, H., Hedges, L. V. & Valentine, J. C. 2009 *The handbook of research synthesis and meta-analysis*. New York, NY: Russell Sage Foundation.
- 26 Genghini, M., Gellini, S. & Gustin, M. 2006 Organic and integrated agriculture: the effects on bird communities in orchard farms in northern Italy. *Biodivers. Conserv.* **15**, 3077–3094. (doi:10.1007/s10531-005-5400-2)
- 27 Kleijn, D. & Báldi, A. 2005 Effects of set-aside land on farmland biodiversity: comments on Van Buskirk and Willi. *Conserv. Biol.* **19**, 963–966. (doi:10.1111/j.1523-1739.2005.00603.x)
- 28 Rundlöf, M. & Smith, H. G. 2006 The effect of organic farming on butterfly diversity depends on landscape context. *J. Appl. Ecol.* **43**, 1121–1127. (doi:10.1111/j.1365-2664.2006.01233.x)
- 29 Rundlöf, M., Bengtsson, J. & Smith, H. G. 2008 Local and landscape effects of organic farming on butterfly species richness and abundance. *J. Appl. Ecol.* **45**, 813–820. (doi:10.1111/j.1365-2664.2007.01448.x)
- 30 Rundlöf, M., Nilsson, H. & Smith, H. G. 2008 Interacting effects of farming practice and landscape context on bumble bees. *Biol. Conserv.* **141**, 417–426. (doi:10.1016/j.biocon.2007.10.011)
- 31 Langellotto, G. A. & Denno, R. F. 2004 Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* **139**, 1–10. (doi:10.1007/s00442-004-1497-3)
- 32 Bancroft, B. A., Baker, N. J. & Blaustein, A. R. 2007 Effects of UVB radiation on marine and freshwater organisms: a synthesis through meta-analysis. *Ecol. Lett.* **10**, 332–345. (doi:10.1111/j.1461-0248.2007.01022.x)
- 33 Kleijn, D. et al. 2009 On the relationship between farmland biodiversity and land-use intensity in Europe. *Proc. R. Soc. B* **276**, 903–909. (doi:10.1098/rspb.2008.1509)
- 34 Andrén, H. 1994 Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**, 355–366. (doi:10.2307/3545823)
- 35 Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. 2002 Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecol. Appl.* **12**, 354–363. (doi:10.1890/1051-0761(2002)012[0354:COSHFT]2.0.CO;2)
- 36 Bianchi, F. J. J. A., Booij, C. J. H. & Tscharntke, T. 2006 Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. B* **273**, 1715–1727. (doi:10.1098/rspb.2006.3530)
- 37 Google Earth 2009 *GOOGLE EARTH 5.1*. Mountain View, CA: Google.
- 38 Büttner, G., Feranec, J. & Jaffrain, G. 2002 *CORINE land cover update 2000. Technical guidelines*. Copenhagen, Denmark: European Environment Agency.
- 39 ESRI 2006 *ARC GIS 9.2*. Redlands, CA: Environmental Systems Research Institute.
- 40 Rounsevell, M. D. A., Ewert, F., Reginster, I., Leemans, R. & Carter, T. R. 2005 Future scenarios of European agricultural land use II. Projecting changes in cropland and grassland. *Agric. Ecosyst. Environ.* **107**, 117–135. (doi:10.1016/j.agee.2004.12.002)
- 41 Adams, D. C., Gurevitch, J. & Rosenberg, M. S. 1997 Resampling tests for meta-analysis of ecological data. *Ecology* **78**, 1277–1283. (doi:10.1890/0012-9658(1997)078[1277:RTFMAO]2.0.CO;2)
- 42 Rosenberg, M. S., Adams, D. C. & Gurevitch, J. 2000 *METAWIN: statistical software for meta-analysis*, v. 2.0. Sunderland, MA: Sinauer Associates.
- 43 Borenstein, M., Hedges, L. V., Higgins, J. P. T. & Rothstein, H. R. 2009 *Introduction to meta-analysis*. Chichester, UK: John Wiley & Sons.
- 44 Rosenthal, R. 1979 The ‘file drawer problem’ and tolerance for null results. *Psychol. Bull.* **86**, 638–641. (doi:10.1037/0033-2909.86.3.638)
- 45 Møller, A. P. & Jennions, M. D. 2001 Testing and adjusting for publication bias. *Trends Ecol. Evol.* **16**, 580–586. (doi:10.1016/S0169-5347(01)02235-2)
- 46 Rosenberg, M. S. 2005 The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution* **59**, 464–468. (doi:10.1111/j.0014-3820.2005.tb01004.x)
- 47 Rosenthal, R. 1991 *Meta-analytic procedures for social research*. Newbury Park, CA: Sage.
- 48 Landis, D. A., Wratten, S. D. & Gurr, G. M. 2000 Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* **45**, 175–201. (doi:10.1146/annurev.ento.45.1.175)
- 49 Rand, T. A. & Louda, S. M. 2006 Predator spillover across the agricultural–natural interface: a threat to native insect herbivores in fragmented landscapes? *Conserv. Biol.* **20**, 1720–1729. (doi:10.1111/j.1523-1739.2006.00507.x)
- 50 Rand, T. A., Tylianakis, J. M. & Tscharntke, T. 2006 Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* **9**, 603–614. (doi:10.1111/j.1461-0248.2006.00911.x)
- 51 Foster, B. L., Smith, V. H., Dickson, T. L. & Hildebrand, T. 2002 Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors. *Oikos* **99**, 300–307. (doi:10.1034/j.1600-0706.2002.990210.x)
- 52 Kremen, C., Williams, N. M., Bugg, R. L., Fay, J. P. & Thorp, R. W. 2004 The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.* **7**, 1109–1119. (doi:10.1111/j.1461-0248.2004.00662.x)
- 53 Holzschuh, A., Steffan-Dewenter, I. & Tscharntke, T. 2008 Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* **117**, 354–361. (doi:10.1111/j.2007.0030-1299.16303.x)
- 54 Albrecht, M., Duelli, P., Müller, C., Kleijn, D. & Schmid, B. 2007 The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *J. Appl. Ecol.* **44**, 813–822. (doi:10.1111/j.1365-2664.2007.01306.x)
- 55 Kohler, F., Verhulst, J., Van Klink, R. & Kleijn, D. 2008 At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *J. Appl. Ecol.* **45**, 753–762. (doi:10.1111/j.1365-2664.2007.01394.x)
- 56 Ricketts, T. H. et al. 2008 Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* **11**, 499–515. (doi:10.1111/j.1461-0248.2008.01157.x)
- 57 Gathmann, A. & Tscharntke, T. 2002 Foraging ranges of solitary bees. *J. Anim. Ecol.* **71**, 757–764. (doi:10.1046/j.1365-2656.2002.00641.x)

- 58 Gabriel, D., Sait, S. M., Hodgson, J. A., Schmutz, U., Kunin, W. E. & Benton, T. G. 2010 Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecol. Lett.* **13**, 858–869. (doi:10.1111/j.1461-0248.2010.01481.x)
- 59 Gabriel, D., Thies, C. & Tscharntke, T. 2005 Local diversity of arable weeds increases with landscape complexity. *Perspect. Plant Ecol. Evol. Syst.* **7**, 85–93. (doi:10.1016/j.ppees.2005.04.001)
- 60 Roschewitz, I., Gabriel, D., Tscharntke, T. & Thies, C. 2005 The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *J. Appl. Ecol.* **42**, 873–882. (doi:10.1111/j.1365-2664.2005.01072.x)
- 61 Robinson, R. A. & Sutherland, W. J. 1999 The winter distribution of seed-eating birds: habitat structure, seed density and seasonal depletion. *Ecography* **22**, 447–454. (doi:10.1111/j.1600-0587.1999.tb00581.x)
- 62 Hunter, M. D. 2002 Landscape structure, habitat fragmentation, and the ecology of insects. *Agric. Forest Entomol.* **4**, 159–166. (doi:10.1046/j.1461-9563.2002.00152.x)
- 63 Thies, C. & Tscharntke, T. 1999 Landscape structure and biological control in agroecosystems. *Science* **285**, 893–895. (doi:10.1126/science.285.5429.893)
- 64 Winfree, R., Williams, N. M., Gaines, H., Ascher, J. S. & Kremen, C. 2008 Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J. Appl. Ecol.* **45**, 793–802. (doi:10.1111/j.1365-2664.2007.01418.x)
- 65 Green, R. E., Cornell, S. J., Scharlemann, J. P. W. & Balmford, A. 2005 Farming and the fate of wild nature. *Science* **307**, 550–555. (doi:10.1126/science.1106049)
- 66 Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M. & Landis, D. 2009 Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Front. Ecol. Environ.* **7**, 196–203. (doi:10.1890/080035)
- 67 Batáry, P., Báldi, A., Sárospataki, M., Kohler, F., Verhulst, J., Knop, E., Herzog, F. & Kleijn, D. 2010 Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agric. Ecosyst. Environ.* **136**, 35–39. (doi:10.1016/j.agee.2009.11.004)
- 68 Billeter, R. *et al.* 2008 Indicators for biodiversity in agricultural landscapes: a pan-European study. *J. Appl. Ecol.* **45**, 141–151. (doi:10.1111/j.1365-2664.2007.01393.x)
- 69 Whittingham, M. J., Krebs, J. R., Swetnam, R. D., Vickery, J. A., Wilson, J. D. & Freckleton, R. P. 2007 Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecol. Lett.* **10**, 25–35. (doi:10.1111/j.1461-0248.2006.00992.x)