

# Interactive effects of landscape context constrain the effectiveness of local agri-environmental management

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## Summary

1. Ecological theory predicts that the effectiveness of local agri-environmental management to enhance species richness at field scales will be the highest at intermediate levels of landscape complexity because of nonlinear effects of landscape context on field-scale diversity.
2. We examined how landscape complexity determined effectiveness of local agri-environmental management in terms of effects on species richness of birds, plants, spiders and bees in 232 extensive and intensive paired fields (112 arable fields and 120 grasslands) from 18 regions located in six European countries.
3. As predicted, landscape complexity enhanced field-scale species richness in a mostly nonlinear (sigmoidal) way, with earlier species richness increases in extensive than in intensive fields along landscape complexity gradients. Length of semi-natural boundaries (for arable fields) and proportion of unfarmed habitat (for grasslands) were the landscape features influencing species richness.
4. The relationships between effectiveness of local management and landscape complexity for all taxa were best described with hump-shaped curves, indicating the highest effectiveness at intermediate landscape complexities.
5. *Synthesis and applications.* We used models to investigate how and why effects of local management intensity on species richness vary along wide gradients of landscape complexity. We conclude that landscape-scale management options should take priority over local extensification measures within agri-environmental programmes. These programmes should follow a hierarchical multi-scale approach directed to address landscape-scale constraints on local diversity.

**Key-words:** Bees, birds, field-scale management, landscape complexity, model testing, non-linear effects, plants, species richness, spiders.

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## Introduction

Agricultural intensification since the 1950s is the main cause of biodiversity loss in agricultural landscapes (Tilman *et al.* 2001; de Heer, Kapos & ten Brink 2005). Modern agriculture increases crop yields through field-scale changes in management, such as increased fertiliser and pesticide inputs, elimination or shortening of fallows and higher mechanization. At the landscape scale, agricultural mosaics have been simplified through regional specialization on a few crops and the removal of non-productive habitats, such as field margins, hedgerows, fallows or woodlots. These changes have reduced the suitability of fields for wildlife and, on a larger scale, the capacity of agricultural landscapes for maintaining species that depend on natural and semi-natural habitats (Benton, Vickery & Wilson 2003; Duelli & Obrist 2003).

Agri-environment schemes (AES) of the European Union Common Agricultural Policy were launched as the main policy instrument for reducing negative effects of agricultural intensification on biodiversity, but their effectiveness for reaching this goal has been questioned (Kleijn & Sutherland 2003; Kleijn *et al.* 2006; Blomqvist, Tamisb & de Snoo 2009; Gabriel *et al.* 2010). AES have proven to be effective for enhancing the abundance of particular species or groups when targeted on specific taxa (Peach *et al.* 2001; Donald & Evans 2006; Kleijn *et al.* 2006; Whittingham 2007; Perkins *et al.* 2011). However, most AES still have the general goal of promoting farmland biodiversity overall (Kleijn & Sutherland 2003; Filippi-Cadaccioni *et al.* 2010).

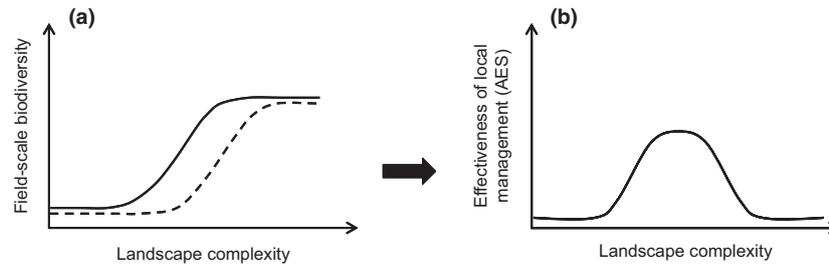
The effectiveness of AES has been questioned because they are implemented at local (usually farm) scales, whereas the impacts of agricultural intensification operate at a range of spatial scales, from fields to whole regions (Benton, Vickery & Wilson 2003; Concepción, Díaz & Baquero 2008). However, individual management options included in AES usually are applied at the field-scale and their effects are generally evaluated at this scale. Factors affecting farmland diversity at different spatial scales are expected to differ among taxa. Larger and mobile organisms, with larger home ranges, are affected by landscape, whilst smaller and less mobile organisms respond to local factors (Concepción, Díaz & Baquero 2008; Gabriel *et al.* 2010; Concepción & Díaz 2011). Furthermore, landscape context can constrain effectiveness of local extensification promoted by AES for improving field-scale species richness (Tscharrntke *et al.* 2005; Concepción, Díaz & Baquero 2008; Batáry *et al.* 2011). Ecological theory predicts that AES effects on species richness will be maximal in landscapes of intermediate complexity (Tscharrntke *et al.* 2005), decreasing to zero in the simplest and the most complex landscapes (Concepción, Díaz & Baquero 2008). This theory is based on underlying nonlinear relationships between landscape complexity and field-scale species richness, which interact with local management effects (Concepción, Díaz & Baquero 2008).

The number of species in agricultural fields generally increases from simple to complex landscapes because semi-natural landscapes contain more diverse resources as well as dispersal corridors. Nevertheless, these landscape effects on local

species richness are expected to be nonlinear rather than linear (Burel *et al.* 1998), having minimum and/or saturation thresholds below and over which no effects are expected (Fig. 1a). It is likely that a minimum amount of unfarmed habitat and dispersal corridors in the landscape is necessary to maintain species inhabiting fields. Thus, extensification measures are expected to be ineffective for increasing field-scale species richness in simple landscapes that are devoid of sources of colonisers (Tscharrntke *et al.* 2005). As landscapes become more complex, local diversity is expected to increase until a saturation point is reached from where no further increases in species richness are expected. Such saturation is likely to be due to continuous recolonization of fields from the complex, species-rich surrounding landscape (Tscharrntke *et al.* 2005), and/or to potential negative effects of unfarmed habitats on open-country organisms inhabiting farmland patches (Díaz & Tellería 1994; Wolff 2005; Gabriel *et al.* 2010), swamping any effect local management may have. Recently, a similar conceptual model focussed on the effects of forests fragmentation on local and regional diversity has been proposed and tested (Pardini *et al.* 2010).

The potential effects of local extensification for increasing local species richness are thus restricted to occur between the two thresholds of landscape complexity (Fig. 1a). The effectiveness of local extensification measures should reach its maximum at intermediate levels of landscape complexity, decreasing in both the simplest and the most complex landscapes (Fig. 1b). The actual location of minimum and saturation thresholds along the landscape gradient and the specific shape of this relationship are expected to differ among taxa depending on their landscape perception and dispersal ability (Steffan-Dewenter *et al.* 2002; Tews *et al.* 2004; Concepción, Díaz & Baquero 2008; Concepción & Díaz 2011). Despite the potential relevance of these hypotheses for agri-environmental policy and associated public spending, they have not yet been tested. If proven, these hypotheses would imply that recovering complexity levels is a prerequisite for the success of local extensification measures in the simplest landscapes, whereas in complex landscapes only initiatives that prevent landscape simplification could be considered effective for biodiversity conservation (Concepción, Díaz & Baquero 2008).

The main goal of this work is to analyse how effects of field management intensity on biodiversity vary along a wide gradient of landscape complexity. As biodiversity measures, we used data on species richness of birds, plants, spiders and bees in 232 extensively and intensively managed paired fields (112 arable fields and 120 grasslands) in 18 regions distributed across six European countries. We first tested which landscape metrics around fields influenced field-scale species richness in each farmland type after accounting for the effects of latitudinal gradient (Willig, Kaufmann & Stevens 2003), local land-use intensity (Kleijn *et al.* 2009) and geographical distribution of study sites (field pairs, regions and countries). Secondly, we examined the shape of relationships between species richness and landscape complexity in paired fields with contrasting management intensity (intensively *vs.* extensively farmed).



**Fig. 1.** Hypothetical nonlinear relationships between a) landscape complexity and biodiversity (species richness) in extensively farmed (continuous line) and intensively farmed fields (broken line) and b) resulting relationship between landscape complexity and effectiveness of local extensification for improving biodiversity (i.e. difference in species richness between extensive and intensive fields). Effectiveness of local extensification would be maximal at intermediate levels of landscape complexity because of landscape-scale constraints to field-scale species richness in both the simpler and the more complex landscapes.

Finally, we examined the shape of the relationships between landscape complexity and the differences in species richness between these paired fields (i.e. ecological effectiveness of field-scale extensification). We expect nonlinear, sigmoidal relationships between species richness and landscape complexity, with earlier inflexion points for extensively managed fields caused by effects of local management on species richness. This would result in Gaussian (hump-shaped) relationships between ecological effectiveness of local extensification and landscape complexity, with maximum effectiveness in landscapes of intermediate complexity (Fig. 1). Location of peak values of local extensification effectiveness along landscape complexity gradients should differ among taxa because of differences in landscape perception and mobility.

## Materials and methods

### STUDY SITES

Testing nonlinear relationships between species richness and landscape complexity requires sampling landscape gradients broad enough to detect such nonlinearity. For this reason, the study area encompasses 18 agricultural regions of six European countries, the three regions in each country being selected to include the most differences in landscape complexity. In all countries except Hungary, fields managed under AES were defined as extensive fields, and fields managed in a conventional way as intensive ones. One of the most widely implemented AES with biodiversity objectives was selected for each country (Kleijn *et al.* 2006): organic farming in cereal crop fields (Germany), extensive management of cereal crop fields for steppe birds (Spain), Ecological Compensation Areas (ECAs) aimed at the conservation of extensively used hay meadows (Switzerland), meadow bird agreements in wet grasslands (the Netherlands) and 6-m-wide grass margin strips along cereal crop fields within the Countryside Stewardship Scheme (United Kingdom). In Hungary, which, at the time of field work, had not yet joined the EU, AES had not been implemented, so that grasslands with low (around 0.5 cows/ha) and higher (1.0–1.2 cow/ha) grazing pressure were used as extensive and intensive fields, respectively. Besides having biodiversity goals, the specific objectives of these AES ranged from preserving specific taxa (Dutch and Spanish schemes) to the protection of farmland biodiversity and environment in general (German, Swiss and Hungarian cases), or even to the creation of a network of semi-natural habitats and corridors to favour wildlife overall (UK's grass margin strips).

Thereby, it is worth noting that each of these AES could be assessed on the basis of their specific objectives, taking into account components of farmland biodiversity other than those considered here (i.e. abundance or population trends of target taxa, species composition of communities). However, this specific assessment is not contradictory with the aim of this work to evaluate how the effects of diversity-oriented AES vary along wide gradients of landscape complexity, focusing on a specific aspect of farmland biodiversity (i.e. species richness) that is widely used in AES evaluations.

In each region, we randomly selected seven fields managed under AES. Each field was matched to a nearby control field, conventionally managed, to minimize differences in factors other than management intensity (i.e. field size and shape, crop type and landscape context). Fields classified as extensive received lower annual nitrogen input (kg N/ha/year) than fields farmed conventionally ( $t_{105} = 7.06$ ,  $P = 6.6e^{-11}$ ). We used nitrogen input as a measure of local land-use intensity because it generally correlates with other management intensity measures (e.g. yield, pesticide applications or livestock density) and has been commonly used to analyse agricultural intensification trends and their impacts on farmland biodiversity (Herzog *et al.* 2006; Kleijn *et al.* 2009). Nitrogen input was calculated from data on N fertilizers applied to fields, which were collected by means of questionnaires to farmers, added to regional amounts of atmospheric nitrogen deposition (EMEP 2005). Atmospheric deposition was included because most nitrogen (mainly ammonia) emissions are caused by the use of fertilizers in agriculture and deposited in the surroundings (for more details, see Kleijn *et al.* 2009).

### SAMPLING PROCEDURE

In spring 2003, we recorded species richness of birds, vascular plants, spiders and bees in study fields following a standardized sampling design (Kleijn *et al.* 2006). Fields within pairs were surveyed by the same observer and on the same date for each taxon. Birds were surveyed four times during the breeding season (between late April and early June) early in the mornings, and their territories were mapped following Bibby, Burgess & Hill 1992 to determine the total number of species found in each field. In grasslands, bird data were collected in 12.5 ha plots including focal fields and their surroundings to standardize sampled surfaces among countries because of large differences in field size (see Table S1 Supporting Information). No data on 12.5 ha plots were collected in Switzerland, where fields were too small, so that for grassland birds only data from Hungary and the Netherlands were available. For plants, we recorded the number of species in the field centre and in the inner field edge, close to (5–10 cm

the field boundary. At both locations, 10 × 1 m plots spaced 5 m apart were located along a transect. Spiders were sampled using one pitfall trap in the inner edge and one in the centre of the field. Traps were opened 2 weeks after full bloom of dandelion *Taraxacum officinale*, a common herbaceous, perennial plant native to Eurasia that is globally distributed. Trapping was performed in two consecutive 2-week periods followed by a final 2-week period separated by a 2-week interval in which traps were closed. This procedure optimises the efficiency of spider surveys in terms of the proportion of species collected out of the total number of species found in fields during the full season (see Duelli, Obrist & Schmatz 1999 for details). For bees, three surveys were carried out along the plant transects in a 1-m-wide and 100-m-long transect along the edge and the centre of each field. Surveys were made by sweep netting (60 sweeps per transect; Banaszak 1980) and searches for foraging individuals (15 min per transect). Sampling was carried out from mid-May to early July between 10:00 and 16:00 h on sunny days. For more details, see Kleijn *et al.* (2006).

Field-scale species richness was measured as the total number of species found during the different surveys for each taxon. This metric is commonly used as a diversity measure in studies evaluating the effects of agri-environmental management because of its local application. Comparing species richness between fields differing only in management intensity allows for direct evaluation of management effects, whereas diversity metrics at higher spatial scales make it difficult to control for confounding effects of other environmental factors (Kleijn *et al.* 2006). However, measures based on field-scale species richness do not account for other diversity components, such as  $\beta$ -diversity, but in our study local species richness was positively correlated with regional species richness for the studied taxa and thus can be considered a robust diversity estimate (Kleijn *et al.* 2006, 2009).

Data on land-use intensity or on the species richness of various taxa were not collected in some fields; therefore, some pairs were excluded from further analyses. This resulted in a sample size of 58 pairs of intensive and extensive cereal crop fields (21 in UK, 19 in Germany and 16 in Spain) and 60 pairs of intensive and extensive grasslands (18 in the Netherlands, 21 in Switzerland and 21 in Hungary).

Landscape metrics were measured using ArcView 3.2 GIS software (ESRI Redlands, California, USA). We selected three metrics closely related to the three main landscape processes influencing field-scale species richness (Concepción, Díaz & Baquero 2008): size of focal fields (ha), as a measure of field configuration; length of boundaries around fields harbouring semi-natural vegetation (m), as a measure of landscape connectivity; and proportion of area occupied by non-productive (i.e. non-farmed) land-uses around fields as a measure of availability of alternative and/or complementary habitats. Length of boundaries and proportion of non-productive land-uses were measured within circular 500-m-radius buffers around centres of focal fields because this distance has been found most suitable to analyse landscape influences on field species richness for a wide range of taxa (Steffan-Dewenter *et al.* 2002; Concepción, Díaz & Baquero 2008; Schmidt *et al.* 2008; Bailey *et al.* 2010).

#### DATA ANALYSES

We fitted generalized mixed effect models (GLMMs; Zuur *et al.* 2009) with Poisson distribution (log-link) to determine what landscape metrics influenced field species richness for each taxon and farmland type. Dependent variables were the field-scale species richness of each taxon. Field pairs nested within regions, nested within countries (country/region/pair), were included as random factors to account for the paired and hierarchically nested sampling design.

Management intensity of fields (extensive vs. intensive grazing or application of AES vs. conventional management) was introduced as a nested factor within field pairs. Farmland type (arable fields or grassland) was introduced as an explanatory factor except for birds, which were analysed separately in arable fields (data collected in study fields) and grasslands (data collected in 12.5-ha plots; see above). The size of focal fields, the length of boundaries and the proportion of area occupied by non-productive land-uses within the 500-m-radius buffers around focal fields were included as continuous explanatory variables. Interactions between farmland type and local management intensity, as well as between landscape metrics and both farmland type and local management intensity, were also fitted in models.

Field-scale diversity is influenced by latitudinal gradients in regional species richness (Willig, Kaufmann & Stevens 2003) and by local land-use intensity (Kleijn *et al.* 2009). We accounted for the possible confounding effects of these variables by including latitude (in decimal degrees) and annual nitrogen input (kg N/ha-year), as estimate of local land-use intensity, for each field as correcting variables in GLMMs. In addition, as our data set came from different countries with variable levels of land-use intensity and landscape complexity, in which distinct AES were applied, we accounted for the possible confounding effects of our design on explanatory variables (e.g. AES, landscape metrics or farmland type). We included the whole hierarchically nested structure of the sampling design (i.e. country/region/pair; see above) as random factors in GLMMs. Moreover, we accounted for the possible varying effects of landscape metrics across countries with different landscape configuration and land-use intensity levels by including an interaction term in the random effects' part of models for each landscape metric (e.g. field size\*country/region/pair). We then compared the models with the interaction terms for each landscape metric with the model without interactions by means of likelihood ratio tests to select the best-fitted models for each response variable. Lack of interactive effects of landscape metrics with the 'study design' term will indicate consistency among countries, regions and field pairs in the analysed relationships in spite of differences in AES, land-use intensity and landscape context among them.

Next, we examined the shape of the significant relationships between landscape metrics and species richness found in GLMMs by fitting linear and different nonlinear Poisson regressions to those relationships. To test our specific hypothesis (Fig. 1a), we compared the fits of linear ( $f(x) = b_0 + b_1x$ ), asymptotic ( $f(x) = b_0 + b_1(1 - \exp(-b_2x))$ ), exponential ( $f(x) = b_0 + b_1\exp(b_2x)$ ) and sigmoidal ( $f(x) = b_0 + b_1/(1 + \exp((b_2 - x)/b_3))$ ) functions. We used models with a quasi-Poisson distribution and identity link function, instead of the classical log-link to fit the linear and the complete set of nonlinear functions to the relationships between landscape metrics and field-scale species richness. To account for overdispersion, effects' estimates were corrected by a variance inflation factor ( $\hat{c} = \sum \text{Pearson } \chi^2 / \text{residual } d.f.$ ; Burnham & Anderson 1998) and  $P$ -values were re-calculated. The fit of models was compared by means of the corrected Quasi-likelihood Akaike's Information Criterion (QAICc), considering that differences in QAICc larger than two units indicate a substantial difference in the goodness of fit of models (Burnham & Anderson 1998). Latitude and log-transformed annual nitrogen input were included as correcting variables in regressions to account for linear latitudinal effects (Willig, Kaufmann & Stevens 2003) and negative exponential effects of local land-use intensity (Kleijn *et al.* 2009) across study sites. Factor 'country' was not included in regressions as effects of landscape metrics were found to be consistent among countries in the former analyses (see below). Poisson regressions between landscape metrics and field-scale species richness were

made separately for extensive and intensive fields to allow for differentiated model parameterization depending on local management intensity. Expected differences in parameters' estimates of sigmoidal regressions between extensive and intensive fields from the hypothetical model (i.e. earlier inflexion points in extensively managed fields than in conventional fields but no differences in the saturation thresholds of fitted sigmoidal models; Fig. 1a) were tested from parameters' estimates and their standard errors by means of Student's *t*-tests. Pair-wise comparisons of the two parameters were only tested for sigmoidal models relating a landscape metric with field-scale species richness of different taxa that were found to be significant in both extensive and intensive fields.

Finally, we examined the shape of relationships between landscape metrics and differences in species richness among paired extensive and intensive fields, a measure of the ecological effectiveness of local extensification, by comparing the fit of Gaussian ( $f(x) = b_0 + b_1 \cdot \exp(-(x - b_2)/2 \cdot b_3^2)$ ) and linear regressions (normal distribution and identity link function). The Gaussian function was selected as the most generalized function describing hump-shaped curves according to the hypothetical model (Fig. 1b). Effects' estimates were corrected by a variance inflation factor, and the fit of models were compared by means of the QAICc. Regressions were only performed for the landscape metrics that had significant effects on field-scale species richness for each taxon according to GLMMs (Table S2 Supporting Information). We accounted for the effects of latitude, average annual nitrogen input of paired fields (log-transformed) and difference in annual nitrogen input between paired intensive and extensive fields by including them as correcting variables in regressions. Average nitrogen input was the surrogate of regional levels of intensification included in GLMMs, whereas the difference in nitrogen input between paired fields is a measure of the local level of extensification because of field agri-environmental management. Differences in the location of peak values of fitted Gaussian models for different taxa along the same landscape complexity gradients were tested by means of multiple pair-wise *t*-tests (with Bonferroni correction) comparing the  $\mu$ -parameter values of Gaussian functions, and the  $\sigma$  parameter as associated standard error, among taxa.

All statistical analyses were performed with R statistical software, using the packages 'stats' (R Development Core Team 2009), for linear regressions; 'lme4' (Bates & Maechler 2010) for GLMMs; and 'bbmle' (Bolker 2009) for nonlinear regressions.

## Results

Landscape had strong effects on the species richness of all taxa after accounting for significant latitudinal, land-use intensity and farmland type effects (Table S2). For arable fields, the length of boundaries with semi-natural vegetation strongly increased species richness of all taxa. For grasslands, this landscape metric increased the species richness of spiders and bees, but decreased species richness of birds. The proportion of non-productive land-uses in the surrounding landscape was positively related to field-scale species richness of birds, plants and bees in grasslands. No significant effects of field size on species richness were found for arable fields or grasslands. Likelihood ratio tests comparing models with a random interaction term for each landscape metric with models without interaction were not significant in any case ( $P > 0.09$ – $0.99$ ; data not shown), thus indicating that relationships found between landscape metrics and species

richness of each taxa can be considered to be valid across countries.

Relationships between significant landscape metrics and field-scale species richness for each taxon were generally best fitted to sigmoidal functions (Table 1), especially for birds (Fig. 2) and plants (Fig. 3). However, better fit to linear rather than to sigmoidal functions and, in some cases, lack of fit to either linear or nonlinear functions were also found, mostly involving arthropods (Table 1). Field-scale species richness was related to the length of boundaries harbouring semi-natural vegetation around fields for all taxa, mainly in arable fields, whereas the proportion of non-productive land-uses affected nonlinearly field species richness of most taxa in grasslands (Table 1).

Pair-wise comparisons between extensively and intensively farmed fields of the inflexion points and upper asymptotes in the five cases in which sigmoidal functions fitted to relationships between landscape metrics and species richness (Table 2) showed a general lack of significant differences in asymptotic values, as well as lower values for the inflexion points for extensive fields, which were significant for birds in arable fields and plants in grasslands (Figs 1–3).

Effectiveness of local extensification (i.e. differences in species richness between paired extensive and intensive fields) was also significantly related to landscape metrics (Table 3). Gaussian relationships, with peak effectiveness at intermediate values of landscape gradients, were always significant. On the contrary, linear relationships were not significant except the effect of length of semi-natural boundaries on effectiveness of local extensification for bees in arable fields, for which the linear model had almost equal fit than the Gaussian (QAICc = 72.5 and 74.5, respectively).

Peak effectiveness (values of the  $\mu$  parameter of the best-fitted Gaussian functions) varied among farmland types, landscape metrics, and taxa (Table 3 and Figs 2 and 3). In arable fields, peak effectiveness for birds was found in landscapes containing shorter lengths of boundaries with semi-natural vegetation than for plants. Peak effectiveness for spiders was found in landscapes with even shorter lengths of boundaries. Lastly, peak effectiveness for bees in arable fields was found with the least length of boundaries. In grasslands, peak effectiveness for bees was found in landscapes containing longer lengths of semi-natural boundaries than for spiders and birds. Finally, peak effectiveness for plants in grassland was found in landscapes containing higher amounts of non-productive land-uses than for birds and bees.

## Discussion

Landscape metrics contributed significantly to explain local species richness of all studied taxa once the effects of latitude, local land-use intensity and geographical location of study fields were accounted for in statistical models. The relative effects of landscape metrics differed between farmland types and among taxa. In arable farmland, the length of boundaries harbouring semi-natural vegetation, an estimate of landscape

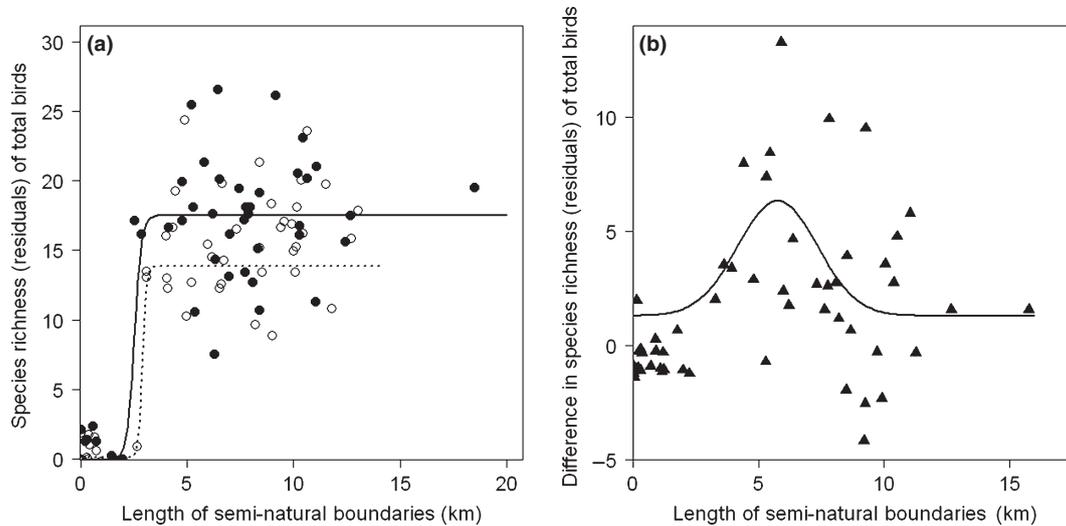
**Table 1.** Results of linear and nonlinear (sigmoidal, asymptotic and exponential) Poisson regressions between landscape metrics (size of focal fields, and length of boundaries with semi-natural vegetation and proportion of non-productive land-uses in 500-m-radius buffers around focal fields) and species richness of birds in focal fields (for arable fields) and 12.5 ha plots (for grasslands), plants, spiders and bees. Models were made separately for arable fields (a) and grasslands (b), as well as for fields farmed extensively or intensively, only considering significant landscape effects (sign in brackets) on field-scale species richness for each taxon (Table S2), after accounting for the effects of latitude and annual nitrogen input. QAICc values and the proportion of deviance accounted by fitted models (%D) are given. Boldface indicates the best-fitted models according to QAICc values, whereas models explaining most deviance are underlined

	Local management	Sigmoidal		Asymptotic		Exponential		Linear		
		QAICc	%D	QAICc	%D	QAICc	%D	QAICc	%D	
<i>a) Arable fields</i>										
Birds (focal fields)										
Length of semi-natural boundaries (km)	(+) Extensive	<b>201-37</b>	<b>77-75</b>	230-83	65-39	264-43	52-41	253-97	55-52	
		<b>239-81</b>	<b>85-31</b>	298-32	68-46	336-72	57-85	326-17	60-10	
Plants										
Length of semi-natural boundaries (km)	(+) Extensive	<b>278-05</b>	<b>71-49</b>	–	–	–	–	–	–	
		<b>202-73</b>	<b>74-00</b>	<b>201-87</b>	<b>73-18</b>	–	–	<b>203-04</b>	<b>71-43</b>	
Spiders										
Length of semi-natural boundaries (km)	(+) Extensive	277-80	41-91	–	–	–	–	<b>272-86</b>	<b>41-93</b>	
		<b>309-85</b>	<b>23-37</b>	–	–	–	–	<b>306-54</b>	<b>20-23</b>	
Bees										
Length of semi-natural boundaries (km)	(+) Extensive	<b>151-49</b>	<b>15-95</b>	–	–	–	–	–	–	
		–	–	<b>150-00</b>	<b>20-63</b>	–	–	<b>149-79</b>	<b>17-68</b>	
<i>b) Grassland</i>										
Birds (12.5 ha plots)										
Length of semi-natural boundaries (km)	(–) Extensive	–	–	–	–	–	–	–	–	
		<b>113-21</b>	<b>39-45</b>	–	–	<b>110-58</b>	<b>38-97</b>	<b>108-67</b>	<b>37-40</b>	
% Non-productive land-uses	(+) Extensive	–	–	–	–	–	–	<b>159-46</b>	<b>52-25</b>	
		–	–	101-68	29-77	–	–	<b>98-52</b>	<b>30-88</b>	
Plants										
% Non-productive land-uses	(+) Extensive	<b>138-33</b>	<b>39-48</b>	<b>138-95</b>	<b>35-96</b>	143-68	30-59	141-07	30-84	
		<b>162-18</b>	<b>28-10</b>	167-55	17-82	–	–	–	–	
Spiders										
Length of semi-natural boundaries (km)	(+) Extensive	<b>295-56</b>	<b>66-63</b>	–	–	–	–	–	–	
		–	–	–	–	–	–	–	–	
Bees										
Length of semi-natural boundaries (km)	(+) Extensive	–	–	–	–	–	–	–	–	
		–	–	–	–	–	–	–	–	
% Non-productive land-uses	Extensive	–	–	–	–	<b>138-18</b>	<b>47-67</b>	–	–	
		–	–	–	–	–	–	–	–	

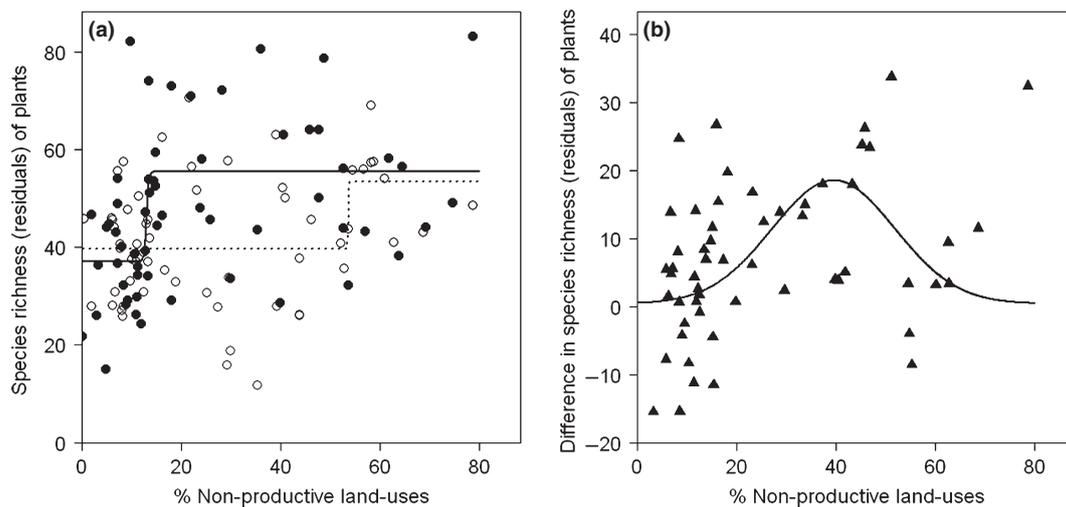
connectivity (Concepción, Díaz & Baquero 2008), had the strongest influence on the species richness of all taxa. In grasslands, the proportion of non-productive land-uses, as an estimate of source or complementary habitats, was the most relevant landscape feature influencing local species richness. Corridors have been found to enhance organism movements through fragmented landscapes when the differences between the fragmented habitat and the matrix are strong, as is the case in arable landscapes (Dennis & Fry 1992; Haas 1995; Marshall & Moonen 2002). The importance of corridors diminishes when habitat-matrix differences are smaller, for example in grassland (Forman 1995; Hudgens & Haddad 2003; but see Baum *et al.* 2004), or for highly dispersive species, for example birds and bees as compared to spiders and plants in arable landscapes (e.g. Concepción, Díaz & Baquero 2008). If dispersal is not constrained to corridors, the distance to source or complementary unfarmed habitats mostly determines local species richness, as has been found for plants and arthropods in intensively managed grassland landscapes (Schmidt *et al.*

2005; Kohler *et al.* 2008). This would explain the positive effects of the proportion of non-productive land-uses in the landscape on species richness of birds, plants and bees in grasslands. Besides acting as corridors, boundaries with semi-natural vegetation in arable landscapes can provide additional resources (food, cover, or unploughed refuges; e.g. Concepción & Díaz 2011; Concepción, Fernández-González & Díaz 2012), which would explain the great importance of boundaries for highly dispersive organisms such as birds.

Landscape effects differed between farmland types for the same taxon, probably due to different requirements of species in each farmland type. The length of boundaries with semi-natural vegetation increased bird species richness in arable fields but lowered it in grasslands. However, length of boundaries increased spider species richness in grasslands. Boundaries with semi-natural vegetation provide additional food resources and safer nesting places within agricultural landscapes for some species (Benton, Vickery & Wilson 2003; Concepción, Díaz & Baquero 2008). However, boundaries can be



**Fig. 2.** Best-fitted regressions to the relationships between length of boundaries with semi-natural vegetation in 500-m-radius buffers around focal fields and (a) total species richness of birds in extensive (filled circles, thick line) and intensive (open circles, dashed line) arable fields and (b) effectiveness of local-scale extensification for improving biodiversity (i.e. differences in species richness between paired extensive and intensive fields; filled triangles, thick line). Data shown are residuals of models including effects of latitude, nitrogen input and, in the case of the model for effectiveness of local-scale extensification, difference in nitrogen input between intensive and extensive fields.



**Fig. 3.** Best-fitted regressions to the relationships between percentage of non-productive land-uses in 500-m-radius buffers around focal fields and (a) species richness of plants in extensive (filled circles, thick line) and intensive (open circles, dashed line) grasslands and (b) effectiveness of local-scale extensification for improving biodiversity (i.e. differences in species richness between paired extensive and intensive fields; filled triangles, thick line). Data shown are residuals of models including effects of latitude, nitrogen input and, in the case of the model for effectiveness of local-scale extensification, difference in nitrogen input between intensive and extensive fields.

detrimental for other species such as open-country birds, as they can fragment rather than connect habitats or increase nest predation risk (e.g. Eglinton *et al.* 2009; Gabriel *et al.* 2010).

Landscape effects can interact with the effects of field management intensity if landscape complexity limits the maximum number of species a given field can sustain (Concepción, Díaz & Baquero 2008). As predicted, landscape effects on field-scale species richness were mostly nonlinear, with lower and upper thresholds (sigmoidal effects; Fig. 1a), thus demonstrating that maximum field species richness was constrained by landscape-scale effects. However, best fit to linear functions and, in

some cases, lack of fit to either linear or nonlinear functions were also found for relationships between landscape variables and species richness of arthropods (spiders and bees). This may have been because of the increasing relevance of local factors to the detriment of regional ones as body size decreases (Gabriel *et al.* 2010; Concepción & Díaz 2011). In fact, the percentage of explained deviance of models accounting for landscape effects on species richness of spiders and bees was lower than for models of birds and plants (Table 1), thus indicating that local factors might be somewhat more relevant than landscape-scale effects.

**Table 2.** Parameters of sigmoidal functions (inflexion point and upper asymptote,  $\pm$ SE) obtained by means of Poisson regression models between landscape metrics and field-scale species richness of taxa for which sigmoidal models fitted best for both extensive and intensive fields (Table 1) in arable fields (a) and grasslands (b), and pair-wise comparisons of these parameters between fields farmed either extensively or intensively. Boldface indicates significant differences in parameter estimates between extensive and intensive fields according to t-tests (\*\*\*\* $P < 0.001$ ; \*\*\* $P < 0.01$ ; \*\* $P < 0.05$ )

	Landscape metric	<i>n</i>	Parameter	Extensive	Intensive	<i>t</i>
<i>(a) Arable fields</i>						
Birds (focal fields)	Length of semi-natural boundaries (km)	56	<b>Inflexion point</b>	<b>2.53 <math>\pm</math> 0.08</b>	<b>2.93 <math>\pm</math> 0.09</b>	<b>3.28****</b>
			Saturation point	17.66 $\pm$ 5.42	13.70 $\pm$ 4.61	-0.20
	Length of semi-natural boundaries (km)	56	Inflexion point	2.51 $\pm$ 0.02	2.7 $\pm$ 0.52	0.36
			Saturation point	6.28 $\pm$ 3.67	5.44 $\pm$ 3.66	-1.14
Plants	Length of semi-natural boundaries (km)	55	Inflexion point	7.02 $\pm$ 2.11	3.11 $\pm$ 0.86	1.29
			Saturation point	52.66 $\pm$ 21.27	44.26 $\pm$ 13.40	-0.64
Spiders	Length of semi-natural boundaries (km)	56	Inflexion point	5.34 $\pm$ 0.01	4.93 $\pm$ 1.00	0.54
			Saturation point	19.54 $\pm$ 8.72	17.21 $\pm$ 7.15	0.26
<i>(b) Grassland</i>						
Plants	% Non-productive land-uses	60	<b>Inflexion point</b>	<b>12.97 <math>\pm</math> 0.27</b>	<b>53.58 <math>\pm</math> 2.1</b>	<b>3.84****</b>
			Saturation point	56.12 $\pm$ 50.62	51.00 $\pm$ 20.38	-1.45

**Table 3.** Results of Gaussian regressions between landscape metrics (size of focal fields, and length of boundaries harbouring semi-natural vegetation and proportion of non-productive land-uses in 500-m-radius buffer around focal fields) and effectiveness of local extensification (i.e. differences in species richness of each taxon between paired extensive and intensive fields) for birds in focal fields (for arable fields) and 12.5 ha plots (for grasslands), plants, spiders and bees. Regressions were made separately for arable fields (a) and grasslands (b) only considering significant landscape effects on field-scale species richness for each taxa (Table S2) and accounted for the effects of latitude, differences in annual nitrogen input between paired intensive and extensive fields and mean annual nitrogen input of field pairs. QAICc values, proportion of deviance accounted by the model (%D) and parameters of best-fitted Gaussian functions (mean and standard deviation,  $\pm$ SE) are given. Models sharing the same letters did not differ significantly in their peak values according to multiple pair-wise comparisons between taxa according to t-test (based on parameters  $\mu$  and  $\sigma$  as peak value and associated SD, respectively, with Bonferroni correction) for the effects of the length of boundaries harbouring semi-natural vegetation in arable fields and grassland (L. boundaries arable fields and grassland columns), and the proportion of non-productive land-uses in grassland (% Non-prod grassland column)

		QAICc	%D	Gauss		L. boundaries arable fields	L. boundaries grassland	% Non-prod grassland
				$\mu$	$\sigma$			
<i>a) Arable fields</i>								
Birds (focal fields)	Length of semi-natural boundaries (km)	75.38	16.41	5.75 $\pm$ 0.16	0.46 $\pm$ 0.69	c		
		66.37	29.27	9.24 $\pm$ 0.02	8.22 $\pm$ 1.21	d		
Plants	Length of semi-natural boundaries (km)	68.79	15.94	5.37 $\pm$ 0.22	0.74 $\pm$ 0.08	b		
		74.53	26.76	0.52 $\pm$ 0.11	1.26 $\pm$ 0.34	a		
Spiders	Length of semi-natural boundaries (km)	74.53	26.76	0.52 $\pm$ 0.11	1.26 $\pm$ 0.34	a		
		74.53	26.76	0.52 $\pm$ 0.11	1.26 $\pm$ 0.34	a		
Bees	Length of semi-natural boundaries (km)	74.53	26.76	0.52 $\pm$ 0.11	1.26 $\pm$ 0.34	a		
		74.53	26.76	0.52 $\pm$ 0.11	1.26 $\pm$ 0.34	a		
<i>b) Grassland</i>								
Birds (12.5 ha plots)	Length of semi-natural boundaries (km)	51.25	8.87	0.68 $\pm$ 0.02	12.42 $\pm$ 2.67		a	
		53.37	5.62	28.97 $\pm$ 1.58	2.06 $\pm$ 41.22			a
Plants	% Non-productive land-uses	72.39	28.07	39.43 $\pm$ 0.36	8.70 $\pm$ 14.92			b
		71.12	8.72	0.20 $\pm$ 0.10	1.66 $\pm$ 0.34		a	
Spiders	Length of semi-natural boundaries (km)	71.12	8.72	0.20 $\pm$ 0.10	1.66 $\pm$ 0.34		a	
		71.12	8.72	0.20 $\pm$ 0.10	1.66 $\pm$ 0.34		a	
Bees	Length of semi-natural boundaries (km)	74.84	7.34	5.91 $\pm$ 0.22	1.38 $\pm$ 0.30		b	
		75.64	20.77	28.67 $\pm$ 0.91	2.74 $\pm$ 2.94			a

Threshold values of sigmoidal functions did not differ among paired fields farmed extensively and intensively, demonstrating that landscape-scale constraints on field species richness were independent of local management intensity. However, inflexion points were reached earlier in extensive

fields, as predicted (Fig. 1a), indicating that local extensification had general positive effects on species richness (Batary *et al.* 2011), albeit within the constraints imposed by landscape complexity (Concepcion, Dıaz & Baquero 2008). As a result of these interactions between local extensification and nonlinear

landscape effects on species richness, hump-shaped curves best described the relationships between effectiveness of local extensification and landscape complexity for all taxa (Figs 2 and 3 and Table 3). As predicted, peak effectiveness differed among taxa and farmland types, but the pattern found was not clearly related to differences in mobility or landscape perception among taxa.

To our knowledge, this is the first attempt to analyse the shape of the relationships between landscape structure, local extensification measures and their effects on an important aspect of farmland biodiversity, that is, species richness. Hump-shaped relationships between landscape complexity and effectiveness of local extensification for increasing species richness, as predicted by Tschardt *et al.* (2005) and Concepción, Díaz & Baquero (2008), could be empirically validated. However, differences among taxa and farmland types in their responses to landscape traits make necessary to further analyse landscape effects in regional contexts to identify landscape elements that should be promoted in particular agrosystems.

Location of maximum effectiveness along landscape gradients also differed among taxa and farmland types. Relationships between different landscape traits and both species richness and effectiveness of local extensification should be analysed along wide gradients within countries and farmland types to accurately identify the location of saturation thresholds and peak effectiveness. This in turn should be used as criteria for the design of specific agri-environmental programmes. More research, both theoretical and empirical, is also needed to analyse landscape effects on aspects of biodiversity other than those considered here, such as species composition and abundance or other diversity components, like regional species pools or species turnover rates among sites. Likewise, landscape effects on target species or groups, habitats or any other element or process whose conservation had been considered relevant within agri-environmental programmes should be additionally evaluated.

Our results have important implications for the design of effective agri-environmental policies aimed at farmland biodiversity conservation. Measures focussed on landscape management (either to restore complexity in simple or to maintain it in complex landscapes) will be generally effective for conserving farmland biodiversity (Fig. 1a). However, the increase in field-scale species richness caused by local extensification measures reaches its maximum at intermediate levels of complexity but falls to zero in both the simplest and the most complex landscapes (Fig. 1b). Recovering landscape complexity levels is thus a prerequisite for the success of AES in the simplest landscapes, whereas in complex agricultural landscapes only initiatives aimed at preventing landscape simplification will be effective. Hence, landscape management options should be prioritized within agri-environmental policies. Specifically, the maintenance of boundaries harbouring semi-natural vegetation in arable land, and patches of non-productive land-uses in grasslands, should be promoted over the wider landscape before considering the application of AES at field scales. However, AES involving the creation or conservation of semi-natural habitats within farms can have

similar effects to landscape management options as far as the uptake by farmers in a region was high enough to influence landscape configuration (Gabriel *et al.* 2010). Likewise, targeted AES that are usually effective in conserving specific taxa could be combined with landscape management options to accomplish particular conservation aims.

We conclude that agri-environmental programmes should adopt a hierarchical multi-scale approach (Evans & Green 2007; Whittingham 2007; Concepción, Díaz & Baquero 2008; Aviron *et al.* 2009). In simpler agricultural landscapes, compulsory measures aimed at recovering complexity levels should be applied to promote farmland biodiversity effectively. Landscape extensification measures could be implemented by means of cross-compliance or wide entry-level schemes (i.e. measures accessible to many farmers with a few simple prescriptions) and should be combined with more targeted field-scale measures when specific conservation objectives are pursued. In complex landscapes with high biodiversity levels, measures that support farmers to maintain rather than to change existing extensive land-use practices could be implemented through, for example, high-nature value farmland (HNVF) programmes to avoid landscape simplification and subsequent biodiversity loss.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Mean values ( $\pm$  SE) and ranges of latitude, annual nitrogen input, landscape metrics (size of focal fields, and length of semi-natural boundaries and percentage of non-productive land-uses in 500-m radius buffers around focal fields) and species richness of studied taxa (birds, plants, spiders and bees) in each country. \* Birds were surveyed in focal fields in arable fields (UK, Germany and Spain), and in 12.5 ha plots in grasslands to standardize sampled surfaces among countries because of large differences in field size. No data on 12.5 ha

plots were collected in Switzerland, so that for the analyses of grassland birds only data from Hungary and The Netherlands were used.

**Table S2.** Results of generalized mixed effect models (Poisson distribution, log-link function) testing for the effects of latitude, annual nitrogen input per field, field management intensity, farmland type (grassland vs. arable fields) and landscape metrics (size of focal fields, and length of boundaries with semi-natural vegetation and proportion of non-productive land-uses in 500 m-radius buffers around focal fields) on field-scale species richness of birds in focal fields (for arable fields) and 12.5 ha plots (for grasslands), plants, spiders and bees. Field pairs nested within regions, nested within countries (country/region/pair) were included as random factor and management intensity (extensive vs. intensive grazing in Hungary and application or not of AES in the remaining countries) as nested factor within field pairs. Interactions of farmland type with local management intensity

and landscape metrics, as well as between local management intensity and landscape metrics, were included in models to account for different effects of these variables depending on farmland type and local management intensity. Z-test statistic is given for each explanatory parameter.  $n = 112$  for birds, bees and spiders and 110 for plants in arable fields.  $n = 120$  for bees and plants, 118 for birds and 108 for spiders in grasslands. Boldface indicates significant effects ( $****P < 0.001$ ;  $***P < 0.01$ ;  $**P < 0.05$ ) and italics marginally significant effects ( $*P < 0.10$ ).

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