RESEARCH ARTICLE

Effects of landscape complexity on the ecological effectiveness of agri-environment schemes

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Abstract Agricultural intensification is a major cause for biodiversity loss. It occurs at field scales through increased inputs and outputs, and at landscape scales through landscape simplification. Agri-environment schemes (AES) of the European Common Agricultural Policy (CAP) aim at reducing biodiversity loss by promoting extensification of agricultural practises mostly at field scales. We present a conceptual model for the relationship between landscape complexity and ecological effectiveness of AES based on (a) non-linear relationships between landscape complexity and abundance and diversity at field scales and (b) four possible interactive scenarios between landscape- and field scale effects on abundance and diversity. We then evaluated whether and how effectiveness of AES interacted with landscape-scale effects of intensification along a landscape complexity gradient established in central Spain. Pairs of cereal fields with and without AES but with the same landscape context were selected in three regions differing in landscape complexity. Effectiveness of AES was

measured as differences between paired fields in species richness and abundance of five target groups (birds, grasshoppers and crickets, spiders, bees and plants). Landscape metrics were measured in 500–m radius circular plots around field centres. Positive, negative and no effects of landscape complexity on effectiveness of AES were found, suggesting that effects of complexity on effectiveness of AES changes from positive to negative along gradients of landscape complexity. Effectiveness of AES for improving biodiversity was then constrained by landscape. Compulsory measures aimed at enhancing or maintaining landscape complexity would enhance the effectiveness of AES for preserving biodiversity in farmed landscapes.

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Introduction

Agricultural intensification is currently considered as a major driver of worldwide biodiversity loss (Benton et al. 2003, Mattison and Norris 2005, Tscharntke et al. 2005). Intensification occurs at the field scale through increased pesticide and fertiliser use, shortened crop-rotations, or machine-driven farming, reducing the suitability of agricultural fields to a

wide range of organisms (Benton et al. 2003; Tscharntke et al. 2005). At the landscape scale, intensification has caused the substitution of most habitats by arable fields or improved grassland (Pain and Pienkowski 1997; Sutherland 2002; Kleijn and Sutherland 2003) and the regional specialization of farmers on a few crops, simplifying landscapes and reducing the possibility of maintaining high numbers of species (Benton et al. 2003; Tscharntke et al. 2005). Intensification at field and landscape scales are tightly connected both during their development (Benton et al. 2003) and, presumably, in their effects on biodiversity (Tscharntke et al. 2005). Recent recognition of this connection between scales has in fact produced a flush of papers incorporating scale issues in the analyses of the effects of agricultural intensification on local biodiversity (see e.g., Jeanneret et al. 2003; Aviron et al. 2005; Clough et al. 2005; Dauber et al. 2005; Gabriel et al. 2005; Purtauf et al. 2005; Roschewitz et al. 2005; Schmidt et al. 2005; Schweiger et al. 2005; Bailey et al. 2007; Batáry et al. 2007; Clough et al. 2007; Holzschuh et al. 2007; Hendrickx et al. 2007). Lanscape complexity usually decreases as agriculture becomes more intensive (e.g., Benton et al. 2003). However, land abandonment also produce a decrease in landscape complexity by reducing the amount and spatial distribution of cultivated habitats in the landscape, reducing the suitability of these landscapes to maintain populations of specialist open-country organisms (Wolff 2005).

Agri-environment schemes (AES) were introduced in the European Common Agricultural Policy (CAP) in the early 1990s to reduce biodiversity loss in agricultural landscapes and to mitigate other harmful effects of modern agriculture. AES provide financial incentives to farmers for adopting environmentally friendly practices mostly at the field scale (i.e., reduction in pesticide and fertiliser applications or delays in harvesting dates). Nevertheless, recent European-wide studies have questioned the effectiveness of AES for biodiversity conservation. Over half the studies showed significant positive effects of AES on the diversity or abundance of target groups such as plants, birds or arthropods, but the remaining studies showed non-significant or even negative effects (Kleijn and Sutherland 2003; Kleijn et al. 2006). More recent studies for countries or schemes not covered in the above reviews also showed similar

mixed effects (e.g., Feehan et al. 2005; Ottvall and Smith 2006; Wilson et al. 2007). One of the reasons suggested to explain the lack of effectiveness of AES is the simplification of agricultural landscapes due to the elimination of uncultivated habitats (Kleijn et al. 2001; Duelli and Obrist 2003). Field boundaries, hedges and fallows satisfy a set of wildlife requirements (refuge, food, breeding sites, etc.) that promote species persistence in agricultural landscapes (Benton et al. 2003) and are assumed to act as corridors for dispersal, facilitating both recolonization and maintenance of populations in agricultural landscapes (Duelli and Obrist 2003). The loss of these habitats would reduce the number of species that could recolonize fields farmed in environmentally friendly ways and hence the effectiveness of AES. The size of scheme-fields and their spatial configuration (distance to other scheme fields or to source habitats) could be more relevant than within-field measures for maintaining diverse arrays of organisms due to fragmentation-related effects on biodiversity (Díaz et al. 1998; Santos et al. 2006).

Landscape effects on local diversity are expected to be non-linear rather than linear (Burel et al. 1998; Tscharntke et al. 2005). No landscape effects are expected below a minimum level of landscape complexity (i.e., amount and spatial distribution of uncultivated habitats). Diversity is expected to increase with complexity only above this minimum threshold (Fig. 1). Positive effects of landscape complexity would eventually level-off after a given level of complexity was reached (Fig. 1). This 'saturation effect' could be due to either recolonization of fields from the surrounding uncultivated landscape (Tscharntke et al. 2005) or to potential negative edge effects of uncultivated habitats on open-country organisms (e.g., Díaz and Tellería 1994; Wolff 2005).

As regards to effectiveness of AES, both landscape complexity around fields and application of AES at field scales are expected to favour biodiversity (Benton et al. 2003), but interactions between both extensification measures have been barely analysed to date (Schmidt et al. 2005). Landscape complexity may either attenuate or magnify differences in species richness and abundance between managed and conventional fields, i.e., effectiveness of AES. Four interactive scenarios are possible (Fig. 2): (a) no interaction between effects of AES and landscape
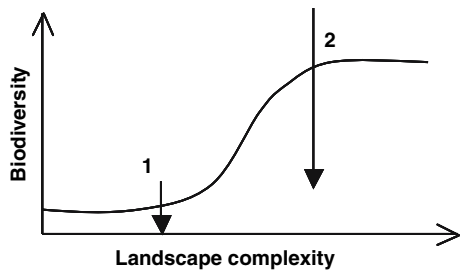
Fig. 1 Hypothetical non-linear effects of landscape complexity around cultivated fields on the biological diversity sustained by such fields. 1: minimum threshold of complexity below which landscapes are too simple for maintaining refuges and/or corridors for wildlife; 2: saturation point of complexity, above which landscapes are so complex that no further effects of complexity are expected

effects; (b) landscape complexity decreases the effectiveness of AES; (c) landscape complexity increases effectiveness of AES; and (d) a combination of the last two, in which interactions between landscape complexity and management effects vary along landscape complexity gradients; landscape

complexity increases effectiveness of AES in simpler landscapes after a minimum threshold of complexity, but decreases effectiveness in the most complex landscapes. The first scenario would predict constant positive effects of AES that would not vary along landscape complexity gradients. The second would predict positive effectiveness in simpler landscapes that would decrease until zero in the most complex landscapes. The third scenario would predict just the opposite, i.e., zero effectiveness in simpler landscapes, and increasing effectiveness with landscape complexity. The last scenario would predict zero effectiveness in both the simplest and the most complex landscapes and positive effectiveness in intermediate landscapes. Effectiveness of AES would increase as landscape complexity increases once a minimum threshold of complexity has been reached until a maximum at intermediate levels of complexity; then, effectiveness of AES would decrease as landscape complexity increases until a point corresponding with the 'saturation point' of diversity.
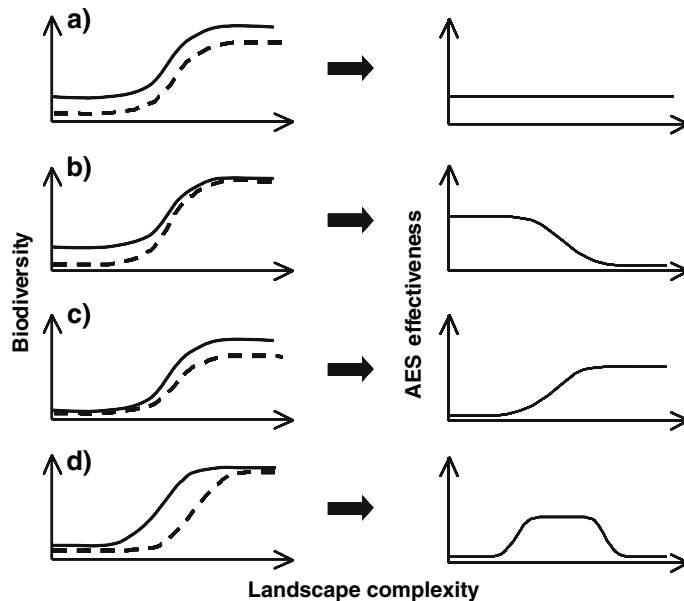

Fig. 2 Hypothetical non-linear relationships between landscape complexity and biodiversity for fields with (continuous line) and without (broken line) AES and the corresponding relationships between landscape complexity and effectiveness of AES depending on the interaction between local management and landscape factors on biodiversity: (**a**) no interaction between both factors: no landscape effects on effectiveness of AES; (**b**) compensation effect of landscape complexity on local management effects on biodiversity: negative effect of

landscape complexity on effectiveness of AES; (**c**) enhancement effect of landscape complexity on local management effects on biodiversity: positive effect of landscape complexity on effectiveness of AES; (**d**) enhancement effect of landscape complexity in simple landscapes and compensation effect of landscape complexity in complex landscapes: positive effect of landscape complexity on effectiveness of AES in simple landscapes and negative effect of landscape complexity on effectiveness of AES in complex landscapes

In central Spain, AES aimed to preserve the populations of endangered steppic birds have proven to be effective for increasing bird abundance, species richness of plants and spiders, and abundance of endangered birds, but had no significant effects on species richness of birds, bees, or grasshoppers and crickets (Kleijn et al. 2006). Similar mixed results according to taxonomic groups were found in other European countries (Kleijn et al. 2001, 2006; Kleijn and Sutherland 2003). As different species groups respond to landscapes at their own spatial scale (Holling 1992; Dauber et al. 2003; Thies et al. 2003; Tews et al. 2004; Aviron et al. 2005), these results could be partly due to interactive effects of landscape complexity on the effects of AES. We evaluate (a) whether effectiveness of AES applied in cereal fields varied along a landscape complexity gradient established in central Spain; (b) whether landscape-AES interactions vary among target groups; and (c) what hypothetical model of landscape-AES interactions was supported by the within-groups and among-groups patterns of interactions between landscape complexity and effectiveness of AES.

Material and methods

Study area

The study was carried out in three agricultural regions with different landscape configuration located in Toledo (Huecas, 40°00′ N, 4°12′ W, 520–580 m a.s.l.; and La Guardia, 39°47′ N, 3°39′ W, 620–670 m a.s.l.) and Ciudad Real (Retuerta del Bullaque, 39°27′ N, 4°22′ W, 710–750 m a.s.l.) provinces, central Spain. The three regions are mostly used for dry cereal production (70–85% area covered by arable fields), mainly barley *Hordeum vulgare* and wheat *Triticum aestivum*, and lie within Important Bird Areas (IBAs) due to the populations of steppic birds they support (Viada 1998).

AES had been applied in the three regions from 1995–1996 to 2003. In Huecas and La Guardia, AES are steppic bird measures applied in extensive cereal croplands, whereas in Retuerta del Bullaque AES are compensation measures applied in the buffer-area of the Cabañeros National Park. The main objective of both AES is the conservation of steppic birds and both include a set of management prescriptions at

field scale that are almost identical (Kleijn et al. 2006). Basically, prescriptions consist on reducing pesticide and fertiliser applications in fields and adjusting the crop calendar to the life cycle of birds. We evaluate these AES because they are the most widespread Spanish scheme (Oñate et al. 1998), so that we could select study areas that differed in landscape complexity but not in the AES applied. Study areas were chosen from the available zones where the evaluated AES were applied by estimating visually landscape configuration (patch size, land-use diversity and presence of remains of natural vegetation) from aerial photographs and field visits. The three regions constitute the broader landscape complexity gradient available, in which Retuerta del Bullaque represented the most complex landscape, Huecas the intermediate and La Guardia the simplest one.

In each of the three regions we selected seven pairs of cereal fields. The field pairs were composed by a field in which the AES had been applied during at least 5 years ('with measures') and a field cultivated in the usual way for the region ('without measures'), that was used as control. The fields within a pair were selected to minimize differences between them in shape, size, crop type and landscape context, being also located close to each other (Kleijn et al. 2006).

Effectiveness of AES

We recorded in each field during spring 2003 the species density (number of species per field) and the abundance (number of individuals or cover) of vascular plants, birds, bees, spiders and grasshoppers and crickets following a standardized sampling design (Kleijn et al. 2006). The five target groups occupy different throphic levels and cover a wide range of body sizes, dispersal strategies and local diversities (species richness). For plants, we measured the number of species and their covers in ten plots of 5 m × 1 m spaced 5 m located in the field edge, and ten more located similarly in the field centre, 50 m away from the nearest field edge. For bees, three survey rounds running parallel to plant plots were carried out from late spring to mid summer between 10.00 h and 16.00 h on sunny days. Surveys were made by sweepnetting (60 sweeps per location per round) and 1-m wide transects (Banaszak 1980;

15 min per location per round). For grasshoppers and crickets we used the same methods as for bees but only once in late summer, when adults were present. Spiders were sampled using one pitfall trap in the edge and one in the centre of the field. Traps were opened 2 weeks after full bloom of *Taraxacum officinale* (30th April in central Spain) and 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 (6 weeks in total; Duelli et al. 1999). Finally, birds were surveyed four times during the breeding season both in focal fields and in 12.5-ha plots including focal fields and their surroundings when focal fields were smaller. For focal fields with AES, plots were either homogeneously covered by fields with AES or consisted of a mosaic of fields with and without AES. For focal fields without AES plots did not contain any fields with AES. Bird territories were subsequently mapped following Bibby et al. (1992).

The effectiveness of AES was measured as the difference in species richness and abundance between fields with and without AES within each pair of each target group. Pooled data for each field was used in the target groups surveyed more than once per field (i.e., all groups except birds). For birds we used data for the 12.5-ha plots only to standardize the surface sampled among field pairs. As species respond to landscape at their own spatial scale depending on their dispersal ability, mobility and on how they perceive landscape context (Holling 1992; Dauber et al. 2003; Thies et al. 2003; Tews et al. 2004; Aviron et al. 2005), the analysis of landscape-scale effects on effectiveness for organisms as different as plants, bees, grasshoppers and crickets, spiders and birds broadened the analysed landscape complexity gradient perceived by the different target groups. Broad complexity gradients are necessary to detect the threshold points hypothesized by our non-linear model for relationships between diversity, effectiveness and landscape complexity (Fig. 1; see also Burel et al. 1998).

Landscape configuration

Digitalized and georeferenced aerial photographs of the three regions were transformed in patches with different land-uses (grassland and set-aside, fallow,

arable fields, buildings and infrastructures, woodlots, olive groves, vineyards, streams and hedges) in a circular buffer area of 500-m around each field centre by means of photo-interpretation and field visits, using a Geografical Information System software (*ArcView GIS 3.2*). Patches only partially overlapped by the circular buffers were included complete in the GIS as several landscape traits were measured on whole patches. We used 500-m circular buffers in order to cover the maximum area around fields without overlapping buffers around different pairs of fields. Linear elements were also mapped in order to characterize types of boundaries between patches within buffers. Boundaries were classified into four types according to their potential suitability for acting as corridors for dispersal: (1) simple boundaries (direct contacts between fields); (2) boundaries with a strip of natural vegetation (contacts between fields with some ground left unploughed); (3) boundaries involving additional natural structures (streams, hedgerows); and (4) boundaries involving additional man-made structures (roads, paths, ditches). Afterwards, a set of landscape metrics (Table 1) were measured using *ArcView GIS 3.2* and its extension *Patch Analyst*. Landscape metrics were measured at two scales. The size and shape of focal fields and the length of each type of boundaries around them were measures at the field scale. Landscape-scale metrics were measured in the 500-m buffers. These metrics referred to landscape composition (cover of different land-uses) and landscape structure (spatial configuration of landscape patches and types of boundaries).

Data analysis

Landscape metrics that differed from normality according to Kolmogorov–Smirnov tests (Underwood 1997) were transformed before analyses. Size and shape metrics were log-transformed, boundary lengths square-root transformed and cover of land-uses arcsin-transformed. We used averages for each pair of fields since our aim was to analyse whether effectiveness, not diversity within fields, was influenced by landscape complexity. Previously, we checked that landscape metrics did not differ between fields within pairs by means of a MANOVA (no differences were expected as we selected pairs on the basis of its similarity in all traits but the application of

Table 1 Landscape metrics used to analyse the dependence of effectiveness of AES on landscape structure around focal fields

Field metrics

  Size of focal field (ha)

  Mean Shape Index: field perimeter divided by the square root of its area adjusted for circular standard. MSI equals one when the field is circular and is larger than one for more complex shapes

  Length of each type of boundary around focal fields (m). Boundary types were (1) simple boundaries (direct contacts between fields); (2) boundaries with a strip of natural vegetation; (3) boundaries involving additional natural structures; and (4) boundaries involving additional man-made structures

Landscape composition metrics, measured on a 500-m buffer area centred in focal fields

  Relative area of each land-use type (%) in the landscape around pairs of fields. Land-uses were grassland and set-aside, fallow, arable fields, buildings and infrastructures, woodlots, olive groves, vineyards, streams and hedges

  Shannon's Diversity Index (SHDI = $-\Sigma p_i * \ln(p_i)$) of the landscape around pairs of fields. Shannon's diversity equals zero when there is only one land-use and increases with both the number of land-uses and the evenness of land-use covers

  Shannon's Evenness Index (SHEI = $SHDI/SHDI_{max} = (-\Sigma p_i * \ln(p_i))/\ln(M)$) of the landscape around pairs of fields. M: number of land-use types. Evenness equals one when all land-uses cover the same surface and tends to zero when a land-use dominates the landscape

Landscape structure metrics, measured on a 500-m buffer area centred in focal fields. Patch traits were measured for whole patches, not only for the area overlapped by the 500-m buffer

  Number of patches: total number of patches in the landscape around pairs of fields

  Mean patch size: average patch size (ha) of patches in the landscape around pairs of fields

  Mean perimeter-area ratio: sum of the perimeter/area ratio of all patches divided by number of patches in the landscape around pairs of fields (m^{-1})

  Edge density: amount of edge relative to the landscape around pairs of fields (m/ha)

  Mean patch edge: average amount of edge per patch in the landscape around pairs of fields (m)

  Area-weighted mean shape index of patches in the landscape around pairs of fields: is the same as the Mean Shape Index defined above with the addition of a weighting factor for patch area applied to each patch that controls for the trend for increasing patch complexity with increasing patch size

  Area-weighted mean patch fractal dimension of patches in the landscape around pairs of fields: mean patch fractal dimension with the addition of a weighting factor for patch area that controls for the positive relationship between patch size and complexity outlined above. This metric approaches one for the simplest shapes and tends to two when shapes are more complex

  Length of each type of boundary in the landscape around pairs of fields (m)

See McGarigal and Marks (1994) for details

AES). The number of landscape metrics was reduced by means of Principal Component Analysis (PCA) to three independent landscape gradients. Using a Varimax normalized rotation, we obtained PCs that covaried with landscape metrics measuring field scale traits (size, shape and type of boundaries), with metrics related to landscape composition (types of land-uses) and with metrics related to landscape connectivity (length of boundaries). This procedure allowed us to analyse the relative contribution of the three main landscape processes that could influence effectiveness (fragmentation-related effects, availability of source populations maintained by uncultivated habitats, and availability of corridors for dispersal).

We tested whether factor scores on the three PCs differed among the three regions by means of one-way ANOVAs. Effects of landscape complexity on effectiveness of schemes were tested by means of one-way ANCOVAs for each target group. Dependent variables were, in each case, the effectiveness of AES for increasing species richness or abundance. The classification factor was the region, and the covariates were the corresponding factor scores on the three PCs of landscape metrics for each pair of fields. Type II sums of squares, which tests for factor and covariate effects after controlling for the influence of all other, were used to account for the fact that field pairs within a region were partly dependent as they were located in similar landscapes (Underwood 1997).

We expected negative or no effects of covariates (Fig. 2d, right) if the full landscape gradient represented by the three study areas lie on the response region or above the saturation point of landscape complexity on biodiversity (Fig. 2d, left), respectively. Significant interactive effects between factor and covariates would indicate that our landscape gradient included some of the hypothesized inflexion points.

Results

Landscape metrics were significantly different among the three regions (two-way MANOVA with pair and region as fixed classification factors; Wilk's $\lambda = 0.0004$; d.f. = 16, 58; $P < 0.0000001$; Fig. 3)

but they did not differ between fields within pairs (Wilk's $\lambda = 0.27$; d.f. = 8, 29; $P = 0.742$). The interaction between the factors pair and region was not significant (Wilk's $\lambda = 0.10$; d.f. = 16, 58; $P = 0.913$). We obtained three PCs from the analysis of average landscape metrics between fields of each pair that explained 55.64% variance of the original data set (Table 2). PC1 represented a gradient of landscape diversity. It associated to its positive extreme landscapes dominated by arable land and to its negative extreme landscapes with high levels of land-use diversity and evenness and high covers of seasonal streams with shrubs and trees. PC1 thus represented an inverse gradient of amount of natural habitats in the landscape and hence of availability of source populations. PC2 covaried with landscape structure metrics. It associated to its positive extreme

Fig. 3 Mean ± SE values for selected landscape metrics that differ between the regions that constitute the analysed landscape gradient: mean size of patches (ha); number of patches; edge density (m/ha); area-weighted mean shape index of patches; area-weighted mean fractal dimension of patches; and proportion of area occupied by natural linear elements (streams and hedges, %). Simple landscape: La Guardia; intermediate landscape: Huecas; complex landscape: Retuerta del Bullaque. See Table 1 for the definitions of landscape metrics
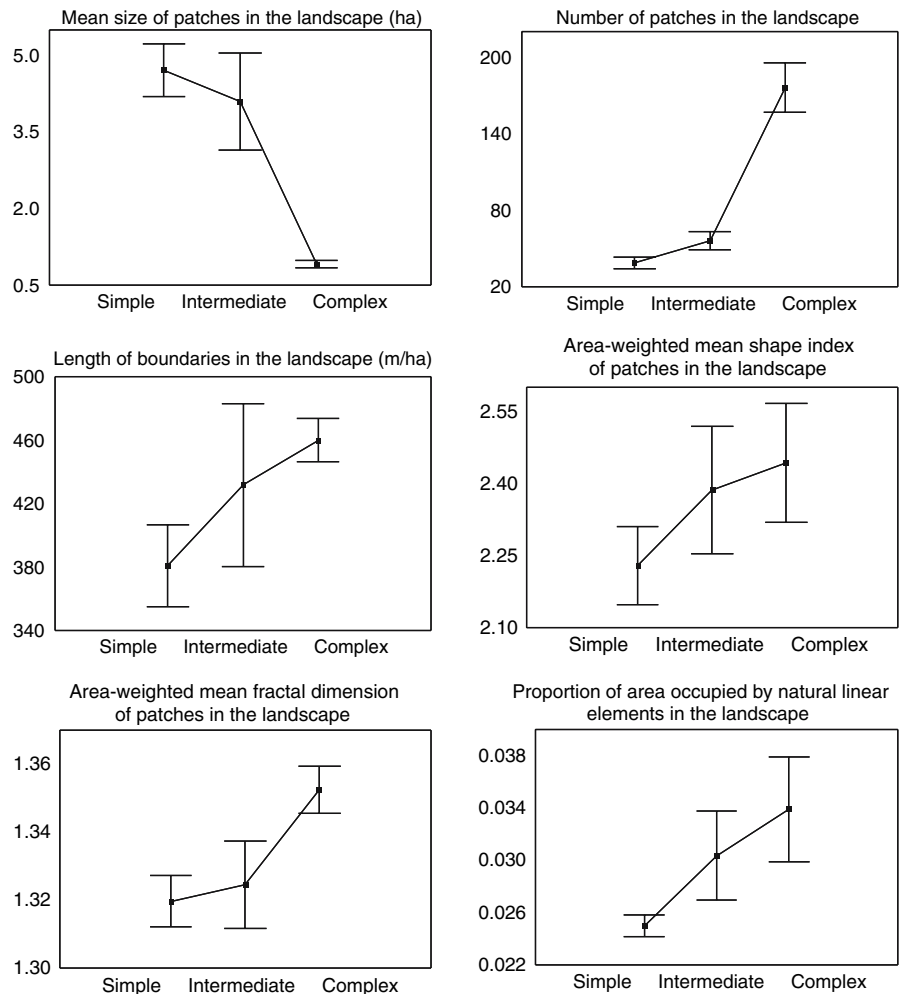
Table 2 Results of a principal component analysis (with Varimax normalized rotation) performed with the average values of landscape metrics between fields of each of the 21 field pairs. Only the factor loadings that were significant at the 0.05 level after a Bonferroni correction (Rice 1989; $\alpha = 0.05/87$ tests) are shown

Variable	PC 1	PC 2	PC 3
Focal field metrics			
Field size			
Length of simple boundaries			
Length of boundaries with a strip of natural vegetation			
Length of boundaries involving natural structures			
Length of boundary involving man-made structures			
Mean Shape Index			0.690
Mean Perimeter-Area Ratio			
Landscape structure metrics			
Number of patches			
Mean patch size		–0.828	
Edge density		0.874	
Mean patch edge		–0.713	
Area-weighted mean shape index		0.775	
Mean Perimeter-Area Ratio			
Area-weighted mean patch fractal dimension		0.812	
Length of simple boundaries			
Length of boundaries with a strip of natural vegetation		0.800	
Length of boundaries involving natural structures	–0.741		
Length of boundary involving man-made structures			
Landscape composition metrics			
Shannon's Diversity Index	–0.906		
Shannon's Evenness Index	–0.896		
Relative area of grassland and set-aside			
Relative area of fallow			
Relative area of arable fields	0.725		
Relative area of buildings and infrastructures			
Relative area of woodlots			
Relative area of olive groves			
Relative area of vineyards			
Relative area of streams	–0.808		
Relative area of hedges and fences			
Eigenvalue	7.94	5.27	2.92
% variance	27.39	18.17	10.07

See Table 1 for the definition of variables

landscapes with high shape complexity and high amounts of boundaries with strips of natural vegetation and to its negative extreme landscapes with high average patch size. PC2 was thus a gradient of landscape connectivity and availability of corridors for dispersal. Finally, PC3 was positively correlated with shape complexity of focal fields. Factor scores on the three PCs of landscape metrics were significantly different among the three regions (one-way MANOVA with region as fixed classification factor;

$F_{2,18} = 11.04$, 5.22 and 5.90; $P = 0.007$, 0.016 and 0.011 for PC1, PC2 and PC3, respectively).

Effects of landscape complexity on effectiveness were mostly non-significant (Table 3). In general, effects of region after removing effects of landscape on effectiveness were not significant either, as well as interactions between region and landscape effects. Significant effects of landscape complexity on effectiveness were negative (i.e., decreasing effectiveness as landscape complexity increased), with only one

exception: positive effects of shape complexity of focal fields (PC3) on differences in spider species richness between fields with and without AES (Fig. 4a). Differences in species richness of breeding birds (Fig. 4b) and, marginally, plants, were however smaller as connectivity (PC2) increased. Landscape connectivity also affected negatively effectiveness of AES for increasing plant abundance (Fig. 4c), whereas increasing shape complexity of focal fields (PC3) decreased marginally effectiveness for increasing the abundance of breeding birds. Differences in diversity between fields with and without AES differ among regions after removing landscape effects only for grasshopper and crickets (Table 3, Fig. 5). Effectiveness was larger in Huecas, smaller in Retuerta del Bullaque and intermediate in La Guardia. Effectiveness of AES for increasing species richness of grasshoppers and crickets also decreased as landscape connectivity (PC2) increased (Table 3); nevertheless, this relationship was partially affected by regional differences in species richness of grasshoppers and crickets between regions (Fig. 5). In fact, significant negative effect of landscape connectivity on effectiveness of AES for species richness of grasshoppers and crickets were only significant in the intermediate region ($b = -0.70$; $t = -3.04$; $P = 0.02$; Fig. 4d). Effectiveness, and effects of landscape complexity gradients on effectiveness, did not differ from zero in the other two regions. Results for endangered species, included in the regional red list of Castilla-La Mancha, were the same as for breeding birds (data not shown), since (a) most birds occupying the study areas were included in that list (23 out of the 29 species found) and (b) no species of plants or arthropods out of the 292 (plants), 55 (bees), 22 (grasshoppers and crickets) and 99 (spiders) found were included in the regional red list (see also Kleijn et al. 2006). The full list of species detected, its conservation status and its abundance in the study areas is available upon request.

Discussion

Studies on landscape effects on farmland biodiversity have usually been focused on either analysing the relationships between landscape complexity and diversity in focal fields or on partitioning field-scale and landscape-scale effects on field diversity (Cushman and McGarigal 2002; Le Coeur et al. 2002; Millán de la Peña et al. 2003; Jeanneret et al. 2003). However, randomly selected focal fields usually differ in unmeasured factors, apart from landscape context and local management, which can also influence local diversity, such as regional species pools and land-use history (e.g., Kleijn and Sutherland 2003). If these unmeasured factors correlate with landscape or current management, conclusions obtained may be wrong. Our paired design controlled for these potential confounding effects by ensuring that fields within each pair differed in local management and not in landscape context. Differences in richness and abundance between paired fields can then be attributed to effects of local management, AES in our case (see Kleijn et al. 2006 for a full discussion). On this basis, the analyses of whether and how landscape context influences the effects of local management is straightforward and not influenced by unmeasured variables.

Results obtained only agreed with predictions of the last model (positive, negative and no effects of complexity on effectiveness depending on the position in the landscape complexity gradient; Fig. 2d), which was based on varying interactions between effects of landscape complexity and effects of local management along landscape complexity gradients. General lack of effects of landscape complexity on effectiveness and the fact that most significant effects found were negative rather than positive would partly support our model if Spanish landscapes were in an advance position in the landscape complexity gradient close to the hypothesized 'saturation point' of biodiversity, an idea further supported by the high species richness found in Spanish agricultural landscapes (Kleijn et al. 2006) and their complex structure as compared to other European countries (Oñate et al. 1998). This interpretation is further supported by differences in effects of landscape complexity on effectiveness of AES depending on landscape components and target groups. Most significant results involved effects of landscape connectivity and, secondarily, shape of focal fields, with no significant effects of landscape composition. These results suggest that in our study areas effectiveness would be more influenced by availability of corridors (Duelli and Obrist 2003) than by availability of source populations maintained by uncultivated habitat patches (Benton et al. 2003). As regards to

Table 3 Results of ANCOVA analyses testing for effects of landscape complexity on the effectiveness of AES, measured as differences in species richness (a) and abundance (b) between paired fields with and without AES

Effect	Spiders	Grasshoppers and crickets	Bees	Bird territories	Plants
(a) Species richness					
Covariates					
PC1	$F_{1,11} = 2.66$ $P = 0.13$ $\beta = 0.75$	$F_{1,11} = 3.54$ $P = 0.098$ $\beta = -0.59$	$F_{1,11} = 1.06$ $P = 0.33$ $\beta = 0.52$	$F_{1,15} = 2.84$ $P = 0.11$ $\beta = -0.74$	$F_{1,10} = 0.88$ $P = 0.37$ $\beta = -0.55$
PC2	$F_{1,11} = 0.09$ $P = 0.77$ $\beta = 0.08$	$\boldsymbol{F_{1,11} = 24.07}$ $\boldsymbol{P = 0.0005}$ $\boldsymbol{\beta = -0.95}$	$F_{1,11} = 0.35$ $P = 0.57$ $\beta = 0.18$	$\boldsymbol{F_{1,15} = 5.43}$ $\boldsymbol{P = 0.034}$ $\boldsymbol{\beta = -0.66}$	$F_{1,10} = 4.48$ $P = 0.060$ $\beta = -0.76$
PC3	$\boldsymbol{F_{1,11} = 5.77}$ $\boldsymbol{P = 0.035}$ $\boldsymbol{\beta = 0.94}$	$F_{1,11} = 0.36$ $P = 0.56$ $\beta = -0.16$	$F_{1,11} = 0.44$ $P = 0.52$ $\beta = -0.28$	$F_{1,15} = 0.24$ $P = 0.63$ $\beta = -0.17$	$F_{1,10} = 0.22$ $P = 0.65$ $\beta = -0.21$
Region	$F_{2,11} = 0.78$ $P = 0.48$	$\boldsymbol{F_{2,11} = 6.50}$ $\boldsymbol{P = 0.014}$	$F_{2,11} = 1.08$ $P = 0.37$	$F_{2,15} = 1.80$ $P = 0.20$	$F_{2,10} = 0.39$ $P = 0.69$
Region × Covariates	$F_{6,5} = 0.46$ $P = 0.81$	$F_{6,5} = 0.70$ $P = 0.66$	$F_{6,5} = 0.19$ $P = 0.96$	$F_{6,9} = 1.60$ $P = 0.25$	$F_{6,4} = 0.04$ $P = 0.99$
(b) Abundance					
Covariates					
PC1	$F_{1,11} = 0.24$ $P = 0.64$ $\beta = -0.23$	$F_{1,11} = 0.39$ $P = 0.54$ $\beta = -0.32$	$F_{1,11} = 0.38$ $P = 0.55$ $\beta = 0.34$	$F_{1,15} = 2.64$ $P = 0.125$ $\beta = -0.70$	$F_{1,10} = 34$ $P = 0.27$ $\beta = -0.54$
PC2	$F_{1,11} = 0.35$ $P = 057$ $\beta = -0.17$	$F_{1,11} = 0.76$ $P = 0.40$ $\beta = -0.27$	$F_{1,11} = 0.00$ $P = 0.96$ $\beta = 0.02$	$F_{1,15} = 2.76$ $P = 0.117$ $\beta = -0.46$	$\boldsymbol{F_{1,10} = 9.00}$ $\boldsymbol{P = 0.013}$ $\boldsymbol{\beta = -0.86}$
PC3	$F_{1,11} = 0.97$ $P = 0.35$ $\beta = 0.40$	$F_{1,11} = 0.84$ $P = 0.38$ $\beta = 0.40$	$F_{1,11} = 0.03$ $P = 0.87$ $\beta = -0.08$	$F_{1,15} = 4.34$ $P = 0.055$ $\beta = -0.75$	$F_{1,10} = 0.28$ $P = 0.61$ $\beta = 0.19$
Region	$F_{2,11} = 0.88$ $P = 0.44$	$F_{2,11} = 0.39$ $P = 0.68$	$F_{2,11} = 0.52$ $P = 0.61$	$F_{2,15} = 2.65$ $P = 0.103$	$F_{2,10} = 0.25$ $P = 0.78$
Region × Covariates	$F_{6,5} = 0.81$ $P = 0.60$	$F_{6,5} = 0.76$ $P = 0.63$	$F_{6,5} = 0.54$ $P = 0.76$	$F_{6,9} = 1.63$ $P = 0.24$	$F_{6,4} = 0.15$ $P = 0.98$

The classification factor was the region, and the covariates were the corresponding factor scores on the three PCs of landscape metrics for each pair of fields (PC1: inverse gradient of landscape diversity; PC2: landscape connectivity; and PC3: shape complexity of focal fields). Boldface indicates significant effects. Differences in degrees of freedom are due to the impossibility of sampling arthropods and plants in some field pairs
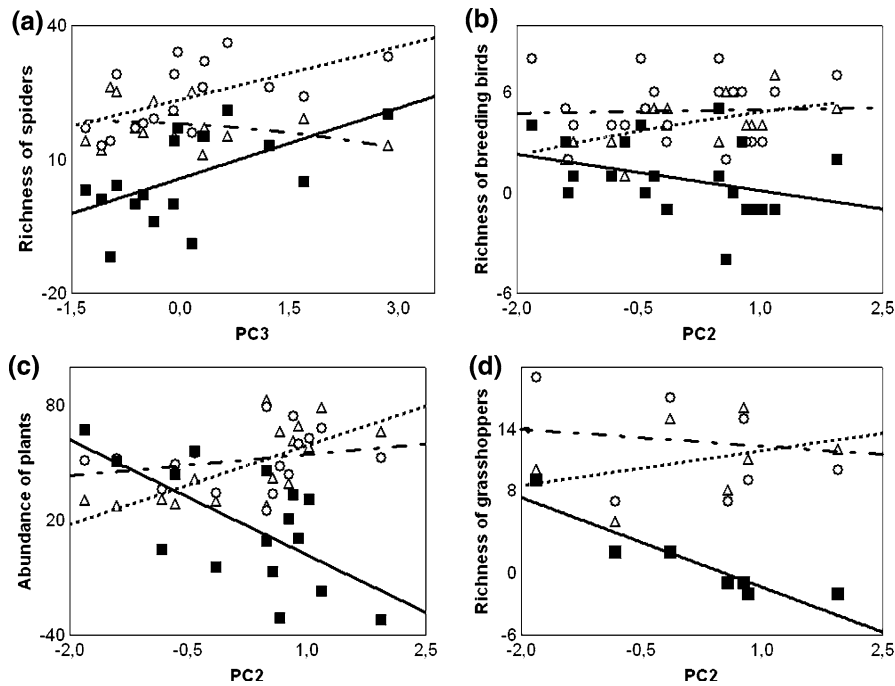
Fig. 4 Scatter-plots of the relationships between landscape complexity (*x*-axis) and both effectiveness of AES (filled squares, thick line) and local diversity or abundance in fields with AES (open circles, pointed line) and without AES (open triangles, dashed line) for the cases of significant effects of landscape complexity on effectiveness. (**a**) increasing effectiveness of AES for increasing species richness of spiders as shape complexity of focal fields (PC3) increases; (**b**) decreasing effectiveness of AES for increasing species richness of breeding birds as landscape connectivity (PC2) increases; (**c**) decreasing effectiveness of AES for increasing abundance of plants as landscape connectivity (PC2) increases; (**d**) decreasing effectiveness of AES for increasing species richness of grasshoppers and crickets as landscape connectivity (PC2) increases in the intermediate region (Huecas)
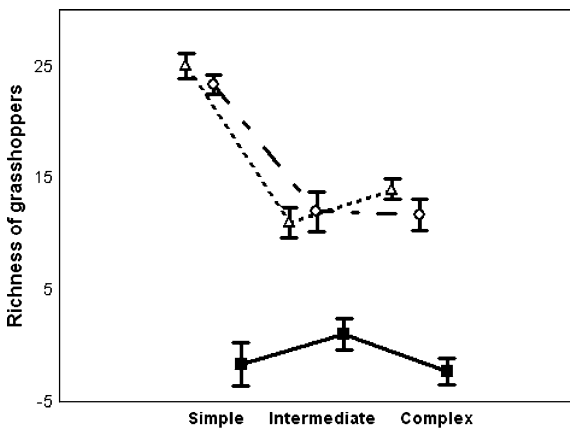

Fig. 5 Mean ± SE values for the effectiveness of AES for increasing species richness of grasshoppers and crickets (filled squares, thick line) and local diversity in fields with AES (open circles, pointed line) and without AES (open triangles, dashed line) in the regions that constitute the analysed landscape gradient. Simple landscape: La Guardia; intermediate landscape: Huecas; complex landscape: Retuerta del Bullaque

target groups, we found positive effects of shape complexity on effectiveness of AES for increasing species density of spiders, and negative or no effects for the remaining groups. Effectiveness decreased with increasing connectivity for species richness of grasshoppers, plants and breeding birds and for abundance of plants. Effectiveness for increasing abundance of breeding birds also decreased with increased shape complexity of focal fields. Finally, no landscape component influenced effectiveness for bees. Differences in mobility among target groups may account for these differences (Holling 1992; Tscharntke et al. 2005). Low mobility of ground-dwelling spiders (Duelli et al. 1990; Downie et al. 1996) could explain why they were influenced by field configuration rather than by surrounding landscape (Dauber et al. 2005) and why they seemed to perceive our study gradient as simpler than organisms with intermediate and high mobility such as

grasshoppers (Reinhardt et al. 2005), plants (Fenner and Thompson 2005; Roschewitz et al. 2005), birds (Holling 1992; Virkkala et al. 2004) and bees (Gathmann and Tscharntke 2002; Steffan-Dewenter et al. 2002).

According to the proposed model, AES would be most effective at intermediate levels of landscape complexity, and effectiveness for improving biodiversity should decrease towards zero in either simpler or more complex landscapes. Tscharntke et al. (2005) developed a similar prediction on the basis of the effects of landscape complexity on landscape-scale species pool sizes. They suggested that effects of local management on biodiversity should only be expected at intermediate levels of landscape complexity because (a) in simpler landscapes species pool sizes are too low for colonisation of scheme fields and (b) in complex landscapes biodiversity is high everywhere and recolinization is continuous. In our model increasing and then decreasing effectiveness (Fig. 2d, right) with landscape complexity are related to different non-linear relationships between landscape complexity and diversity in fields with and without AES that are forced to converge at the threshold and saturation points of the non-linear model (Fig. 2d, left). A straightforward test of our model can be done by analysing, for each target group, the shape of the relationships between field scale diversity and landscape complexity for fields differing in local management. This test would require data for paired fields located along a broader gradient of landscape complexity than the one analysed here, covering specially the intermediate and simpler regions for most target groups. Nevertheless, data presented here partially support the proposed model, as positive and negative effects of landscape complexity on effectiveness of AES were associated to divergent and convergent relationships, respectively, between landscape complexity and diversity or abundance of organism in fields with and without schemes (Fig. 4).

Effectiveness of AES for improving biodiversity seems to be constrained by landscape complexity in both the simplest (Kleijn et al. 2001; Duelli and Obrist 2003) and the most complex landscapes (Tscharntke et al. 2005). Thus, AES would be most effective at intermediate levels of landscape complexity, whereas measures aimed at increasing, in simpler landscapes, or preserving, in complex ones,

landscape complexity would be more effective than management prescriptions at the field scale to promote biodiversity in agricultural landscapes. Many authors have suggested that AES should include measures aimed at both field- and landscape-scale extensification (Baudry et al. 2000; Benton et al. 2003; Jeanneret et al. 2003; Ouin et al. 2004; Aviron et al. 2005; Clough et al. 2005; Dauber et al. 2005; Gabriel et al. 2005; Purtauf et al. 2005; Roschewitz et al. 2005; Schmidt et al. 2005; Schweiger et al. 2005; Batáry et al. 2007; Clough et al. 2007; Holzschuh et al. 2007; Hendrickx et al. 2007). Nevertheless, AES are constrained to be applied mostly at field scales because they are based on voluntary agreements with landowners, a fact that limits its potential for increasing landscape complexity (Kleijn and Sutherland 2003; Kleijn et al. 2006; see also Díaz et al. 1998 for the case of reafforestations). Application of AES in complex agricultural landscapes could be considered to be effective in terms of biodiversity conservation, however, if they prevent landscape simplification and biodiversity loss due to land abandonment (e.g., Herzon and O'Hara 2007). This 'preservation' function can be constrained, however, due to low uptake by reluctant farmers to change farming practices which are already extensive (e.g., Oñate 2005 for the Spanish cereal croplands analysed here). Compulsory measures applied across the whole countryside rather than voluntary measures applied at field scales seems thus be needed for both enhancing landscape complexity in intensified agricultural landscapes and to maintain complexity in face of risks of abandonment in extensive landscapes, a pre-requisite for significant effectiveness of AES. Cross-compliance measures designed as a basis for AES application (Oñate 2005), as well as AES including compulsory and voluntary measures within an integrated framework of multi-scale effects of land-use changes on farmland diversity such as the British Countryside Stewardship Scheme, would be more effective than AES alone for preserving biodiversity in farmed landscapes both for ecological and socioeconomic reasons (e.g., Carey et al. 2005). Our conceptual model on the interactions between landscape- and field-scale effects of agricultural land-use intensity provides a biological basis for the need of integrated conservation policies aimed at preserving biological diversity in agricultural landscapes.

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