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Field, landscape and regional effects of farmland management on specialist open-land birds: does body size matter?

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Abstract

Farmland birds have suffered significant declines in the last decades due to agricultural intensification. Agri-environment schemes (AES) aim to reverse this process by promoting “nature friendly” practises at the field-scale. AES based on the habitat requirements of target species have usually been successful, but the concurrence of species groups with contrasting habitat requirements (guilds) makes the design of successful measures for the whole bird community difficult. The effectiveness of AES is also constrained by landscape and regional effects not addressed by its field-scale application. Effects acting at different spatial scales could differ among bird species depending on basic life-history traits such home range size and landscape perception, which should covary with body size. We are not aware, however, of any study which investigates whether relative effects at different spatial scales could vary predictably within bird guilds. We analyse whether relative effects of within-field (including AES application), landscape and regional factors on open-land birds differ according to body size. Large birds were mostly affected by regional and landscape factors, whereas for small birds landscape and within-field factors were important. Hence, relative effects at changing spatial scales showed predictable variation according to bird size within this endangered and specialised farmland guild. These size-dependent effects should be taken into account for the design of more effective, integrated multi-scale strategies for the conservation of farmland birds.

Keywords: Agri-environment schemes; Bird size; Landscape composition; Landscape connectivity; Open-land birds; Regional effects.

1. Introduction

In the last decades farmland birds have suffered a significant decline due to agricultural intensification across the world (Donald et al., 2001, 2006; Tilman et al., 2001). Agri-environment schemes (AES) were conceived to reverse this process by supporting farming practises compatible with environment and wildlife conservation. Nevertheless, they have turned out to be less ecologically effective than expected (Kleijn and Sutherland, 2003; Kleijn et al., 2001, 2006). AES have proven to be generally effective when their objectives are well-defined and their prescriptions are based on the habitat requirements of target species (Donald et al., 2006; Kleijn et al., 2006; Peach et al., 2001; Whittingham, 2007). However, most AES still have the general goal of preserving farmland biodiversity (Filippi-Codaccioni et al., 2010; Kleijn and Sutherland, 2003) and are evaluated on the basis of their ability to enhance the abundance and species richness of all farmland birds present in a given region (Filippi-Codaccioni et al., 2010). The widespread concurrence of species groups with contrasting habitat requirements (i.e. nesting and foraging guilds) can however limit the effectiveness of these AES. In this sense, prescriptions that benefit ecotonic birds requiring woody vegetation around fields may be neutral or even harmful for other guilds, such as open-land specialists that may suffer from increased predation risk coming from woody patches (Díaz and Tellería, 1994; Díaz et al., 1998; Gabriel et al., 2010). On this basis, both the design of diversity-oriented AES and the evaluation of its effectiveness should take into account the guild structure of target groups, either considering the degree of specialisation of each bird species within regional communities (Filippi-Codaccioni et al., 2010) or focussing on endangered guilds (e.g. meadow or steppe birds; Kleijn et al., 2001; Llusía and Oñate, 2005).

The effectiveness of local agri-environmental management for increasing diversity of target groups is additionally constrained by landscape-scale and regional effects, that field-scale conservation measures do not address properly (Batáry et al., 2011; Concepción et al., 2008; Tscharntke et al., 2005). Maximum effectiveness of field-scale extensification is found in landscapes of variable complexity according to farmland type, community traits and taxa (Batáry et al., 2011). In any case, effects of factors affecting farmland diversity at different spatial scales are expected to differ among taxa according to their perception ranges and dispersal ability (Aviron et al., 2005; Steffan-Dewenter et al., 2002; Tews et al., 2004). Larger and more mobile organisms, with larger home ranges, tend to be mostly affected by surrounding landscape, whilst smaller and less mobile organisms would respond mainly to

factors acting in close proximity (Concepción et al., 2008; Gabriel et al., 2010; but see also Batáry et al., 2011).

Within a taxon, landscape-scale effects have been found to differ among guilds because of contrasting habitat requirements (Barbaro and van Halder, 2009; Batáry et al., 2007; Concepción and Díaz, 2010). For instance, the species richness of open-land birds in Spanish cereal crop fields was influenced by the amount of cropped area in the surrounding landscape, whereas the amount of cropland had no significant effects on the species richness of ecotonic birds (Concepción and Díaz, 2010). Likewise, open-land birds were more benefitted than ecotonic birds by the application of AES (Concepción and Díaz, 2010). We are not aware, however, of any analyses on whether relative effects of farmland management at different scales could vary predictably within bird guilds.

In this study we analyse the effects of factors acting at different spatial scales (field, landscape and region) on the abundance and species richness of birds of the open-land guild that occupy dry cereal croplands of central Spain. Specifically, we test whether the relative contribution of effects acting at increasing spatial scales vary consistently according to the body size of birds within this guild. Spanish dry cereal croplands harbour important populations of most farmland birds of European conservation concern (Butler et al., 2010), whose body sizes range from the 10 g of zitting cisticolas *Cisticola juncidis* to the 15 kg of male great bustards *Otis tarda* (Concepción and Díaz, 2010). AES implemented in this agricultural system are specifically aimed at the conservation of specialists open-land birds, which nest and forage on the ground (Llusía and Oñate, 2005). We hypothesize a decrease in the relative effects of field-scale traits with increasing size of bird species within the same guild, together with an increase in the relative effects of factors acting at larger spatial scales, because larger size would imply larger home ranges of individual species and a coarser perception of landscapes (Gabriel et al., 2010; Holling, 1992). If proven, these body-size effects would imply a serious constraint to the capacity of field-scale extensification promoted by AES for preserving large-sized, endangered steppe birds on farmland, also emphasizing the need to promote conservation strategies at the wider landscape scale.

2. Methods

2.1. Study sites

The study area encompasses three agricultural regions of Castilla-La Mancha (central Spain) dedicated to extensive dry-cereal farming. The three areas are close to each other (60-80 km) but differ in landscape configuration. Retuerta del Bullaque (N, 4°22' W, 710–750 m a.s.l.) represents the most complex, fine-grained landscape; Huecas (40°00' N, 4°12' W, 520–580 m a.s.l.) an intermediate landscape; and La Guardia (39°47' N, 3°39' W, 620–670 m a.s.l.) is the simplest, most coarse-grained landscape. Differences in landscape complexity were due to increasing mean patch size and decreasing mean number of patches, boundaries and patch complexity metrics from the most complex to the simplest area (see Concepción et al., 2008 for details). The three regions harbour important populations of open-land birds of conservation concern (Viada, 1998). AES aimed at the conservation of this guild have been applied in the three study areas since 1995–1996. AES mainly operate on a set of field-management prescriptions aimed at enhancing food availability by reducing pesticide and fertiliser inputs, as well as at decreasing adult and nestling mortality of ground-nesting birds by adjustments of the farming calendar to the life cycle of birds (Table 1; Kleijn et al., 2006; Llusía and Oñate, 2005). These AES have proven to be effective for increasing bird abundance, but not species richness, of both common and endangered birds (Concepción and Díaz, 2010; Kleijn et al., 2006).

Seven pairs of fields including one field in which AES had been applied during at least five years and a control field farmed conventionally were established in each study area. Paired fields were located over an area of 20-30 km² in each region. Fields within pairs were selected close to each other (mean distance between centres of paired field: 660 m; range 256-2214 m), and were as similar as possible in factors other than local management potentially affecting bird abundance and species richness (i.e. crop type, field size and shape, and surrounding landscape; Kleijn et al., 2006). Field traits and landscape context did not differ between paired fields (see Concepción et al., 2008 for details).

2.2. Data collection

Birds were surveyed during the breeding season of 2003 and their territories were mapped following Bibby et al. (1992). Each pair of fields was visited four times by the same observer and on the same dates between late April and early June at 7-10 day-intervals (Kleijn et al., 2006). Observers walked slowly around and through the study fields, for around 20 minutes per field, early in the mornings of sampling dates. All bird contacts were mapped on aerial

138 photographs, also noting behaviours indicative for territorial activities (Bibby et al., 1992).
139 Mapping was concentrated in a representative 12.5 ha section of study fields when they were
140 larger. Size of sampled fields varied between 6.32 and 35.07 ha (median: 10.90 ha) and did
141 not vary among fields within pairs (Concepción et al., 2008). From mapped observations we
142 determined the number of species and the number of territories of birds breeding in each
143 study field (species richness and abundance of territory-holding birds) and the total number of
144 species and individuals found both breeding and foraging in such fields during the four
145 surveys (species richness and abundance of all birds). Openness of the sampled landscapes,
146 sampling schedules covering the whole breeding period of the bird community, and the strong
147 territorial behaviour of the species involved ensured unbiased estimates of species richness
148 and densities of bird communities in the paired study fields (Díaz and Tellería, 1994; Reino et
149 al., 2010). We focused on the open-land guild, which is composed of the bird species that
150 breed and forage on the ground. This guild includes almost all Spanish steppe birds of
151 conservation concern (Bota et al., 2005). Bird species were classified as small (< 50 g),
152 medium-sized (50 g – 500 g) and large (> 500 g) according to their body mass (Cramp, 1998).

153 Species richness and cover of weeds and abundance of grasshoppers and crickets in
154 study fields were recorded as estimates of food availability (Bota et al., 2005; Concepción and
155 Díaz, 2010; Llusía and Oñate, 2005). Plants were sampled in 10 plots of 5 m $\times$ 1 m located
156 parallel to the field edge along the first row, and ten more in the field centre, 50 m away from
157 field edges (Kleijn et al., 2006). Grasshoppers and crickets were surveyed by sweep-netting
158 (60 sweeps) along one survey transect 1 m wide, parallel to plant plots, between 10:00 h and
159 16:00 h on sunny days. Sampling was done between late May and early July, just before
160 harvesting the earlier-harvested field of each pair. Again, each pair of fields was always
161 surveyed by the same observer and on the same date (Kleijn et al., 2006). Weed cover was
162 finally discarded as it was strongly correlated with plant species richness (Concepción and
163 Díaz, 2010).

164 Landscape metrics were obtained from digitalized aerial photographs using the GIS
165 software ArcView 3.2 (ESRI, 2000). We measured size (in ha) of study fields, total length of
166 boundaries with natural or semi-natural vegetation (mostly grassy strips between fields and,
167 occasionally, shrubby and riparian vegetation; in m) in 500-m circular buffers centred on
168 focal fields, and the proportion of cropped area in buffers. These metrics summarize the three
169 main independent components of landscape structure of the three study areas: field
170 configuration, landscape connectivity and landscape composition (Concepción et al., 2008).
171 Field configuration refers to effects of fragmentation on crop specialists, and was summarized

by field size as it covaries with other fragmentation-related traits such as field shape. Landscape connectivity was summarized by amount of boundaries, which covaries with patch complexity metrics, and landscape composition by amount of cultivated lands, which covaries with land-use diversity. These three landscape metric were statistically independent (Concepción et al., 2008) and have been found to influence differentially the abundance and species richness of farmland bird guilds (Concepción and Díaz, 2010).

2.3. Data analysis

We used generalized linear mixed effect models (GLMM; Pinheiro and Bates, 2000), with Poisson or zero-inflated Poisson (for data with excess zeros) distributions and log-link functions. This approach aimed at compensating for overdispersion caused by excess zeros and potential effects of small samples sizes on statistical power (Zuur et al., 2009). Overdispersion parameters were calculated to ensure that there was no additional overdispersion caused by the count part of the data (Zuur et al., 2009). Response variables were species richness and abundance of territory-holding birds and all birds, both breeding and foraging, in study fields. We established three sets of explanatory parameters dealing with within-field, landscape- and regional traits potentially influencing farmland birds. The first set included application or not of AES, species richness of plants and abundance of grasshoppers and crickets. Species richness of plants and abundance of grasshoppers and crickets were higher in fields with AES than in conventional fields (Kleijn et al., 2006). We then included them as estimates of food availability in the models in order to separate potential effects of AES caused by increased food availability from effects caused by reduced risk of bird mortality (Table 1; Concepción and Díaz, 2010). The second set of predictors included size of study fields, length of semi-natural boundaries and proportion of cropped area within 500-m buffers around focal fields. Lastly, study area was also included to account for regional effects. The three set of predictors were orthogonal by design, as ranges of field-scale traits were homogeneously covered along levels of landscape traits and across study areas (Concepción and Díaz, 2010). Field pairs were included as random factors in models. Statistical analyses were performed with R (R Development Core Team, 2009) using the extension ‘glmmADMB’ (Skaug et al., 2006).

The model with the best subset of predictors for each response variable was selected using the likelihood ratio test. Explanatory parameters were dropped from models step-

wisely, computing the likelihood ratio and removing variables with non-significant values until all parameters included in each model when dropped produced a significant decrease in its likelihood (Pinheiro and Bates, 2000). Effects of parameters included in the best fitted models for each response variable can be considered additive effects, as variables tested were orthogonal by design. We thus used the type III sums of squares, which estimates the effect of each explanatory parameter after controlling for the effects of the remaining predictors included in the model. Analyses were made for open-land birds of each body size group (small, medium and large) separately in order to analyse whether responses of birds to field- and landscape-scale traits varied among body-size groups.

3. Results

We found a total of 42 species of birds in our study fields. 19 out of these were open-land species, with 5-8 species in each size group (Table 2). All open-land species detected were considered as steppe birds, which depend on open landscapes maintained by agricultural use (Bota et al., 2005), with the exception of the few woodlarks *Lullula arborea* and mallards *Anas platyrhynchos* found in fields. However, removal of data on these two species did not change results. Most individuals and breeding territories of open-land birds belonged to small species (76% and 71%, respectively), and the rest were more evenly distributed among medium-sized (14% and 17%) and large birds (10% and 12%). Regarding threat status, 87% individuals and 84% breeding territories belonged to endangered species according to regional criteria. All species within the large and small groups were threatened. Large species were all categorized as Vulnerable whereas the small ones were included in a lower risk category (Special Interest). On the contrary, only 5% of individuals and territories belonged to endangered species in the medium-size group, which was dominated by game birds.

Results of GLMMs (Table 3; Fig. 1) showed that the relative contribution of factors acting at different spatial scales on open-land bird communities changed among body size groups and community parameters (species richness vs. abundance). Species richness of small birds was positively affected by landscape traits around fields (length of boundaries with semi-natural vegetation and percentage of cropped area), with additive effects of plant species richness within fields on territory-holding birds. Species richness of large birds was only influenced by regional factors, and richness of medium-sized birds did not vary according to regional, landscape or within-field traits. The abundance of open-land birds was mainly

influenced by regional and landscape-scale effects for all body size groups, with significant additive effects of the application of AES for small birds only. Field size decreased the abundance of medium-sized birds, length of semi-natural boundaries around fields increased the abundance of small and medium-sized birds, and percentage of cropped area around fields increased the abundance of small and large birds. The influence of landscape-scale traits disappeared when considering breeding territories only. There were significant field-scale effects on the abundance of breeding small and medium-sized birds (application of AES and plant species richness, respectively), whereas the abundance of large breeding birds was exclusively affected by study area. Thus, field-scale effects mediated by the application of AES were only significant for small and, to a lesser extent, medium-sized birds. Effects of the landscape surrounding fields tended to decrease its influence as body size increased, especially on species richness, and regional-scale effects were the main factors influencing large birds.

Best fitted models for the different body size groups accounted unequally for the data deviance (Table 3, Fig. 1). For large birds, explained deviance was slightly larger for the species richness and abundance of all birds (24% and 21%, respectively) than for territory holding birds (17% and 18%). Likewise, percentage of explained deviance was higher for the abundance of all birds than for breeding territories in the case of medium-sized (21% and 7%) and small birds (30% and 23%). In addition, no deviance was explained by models for species richness of medium-sized birds, as no significant effects were found. For small birds, explained deviance was lower for species richness of both all and territory-holding birds (9% and 13%, respectively) than for their abundances.

4. Discussion

Our results demonstrate consistent differences in the relative effects of within-field, landscape and regional traits on the abundance and species richness of open-land birds according to body size. Overall, the species richness and abundance of open-land birds were mostly determined by regional factors, especially for the largest and most endangered birds (Figure 1). Landscape-scale traits significantly influenced the abundance of all open-land birds, but their influence on species richness was only significant in the case of small birds. Finally, field-scale effects had the lowest relevance for open-land birds, and their relative contribution decreased as body size increased. These results supported the hypothesis that different species

within the same taxa and guild can respond to factors acting at different spatial scales according to their ranges of perception.

Small species tended to respond positively to implementation of AES, both directly, through reduced mortality, and indirectly, through increased food availability within fields (Kleijn et al., 2006; Llusía and Oñate, 2005). In the case of medium-sized birds, field-scale effects were mostly marginal and related to increased food supply (weed species richness and, probably, cover; Concepción and Díaz, 2010). Thus, the already reported positive effects of AES on open-land birds (Concepción and Díaz, 2010; Kleijn et al., 2006) consisted of the enhancement of local breeding populations of small and medium-sized birds, whereas the largest and most endangered bird species responded to factors acting at wider scales.

Relative contribution of the different landscape traits affecting open-land birds also differed among body-size groups. Positive effects of the proportion of cropped area around focal fields for small and large birds highlight the need to avoid the abandonment of extensive farming systems for open-land birds (Concepción and Díaz, 2010; Morgado et al., 2010; Sirami et al., 2008). This point is especially important for the largest and most endangered species, such as great bustards, which are intimately bounded to cereal crops for both nesting and foraging (Morales et al., 2006; Moreira et al., 2004). The amount of field boundaries with semi-natural vegetation around fields had also positive effects on small and medium-sized birds. This result emphasizes the need for the conservation of linear remnants of semi-natural vegetation within agricultural landscapes, as they provide additional food resources and safer nesting places (Benton et al., 2003; Butler et al., 2007; Casas and Viñuela, 2010; Evans and Green, 2007). Field size influenced negatively the abundance of medium-sized birds, a result that may also have arisen from a dependence on field boundaries for nesting that would limit the bird's ability to exploit large fields (Parish et al., 1995). This process has in fact been proven for red-legged partridges (Borrallho et al., 1999; Casas and Viñuela, 2010), the dominant species of the medium-sized group.

Finally, we found strong differences among study areas for all bird groups, which were not related to field- or landscape-scale traits. Differences among study areas were especially marked for large, endangered birds, which were almost exclusively affected by differences among regions. These regional effects cannot be attributed to either biogeographic gradients or regional differences in general habitat suitability, as the three study areas were located in close proximity within core areas for large open-land birds (e.g. Suárez-Seoane et al., 2002; Viada, 1998). Regional effects were also particularly relevant for the abundance of bird territories, for which explained deviance was in addition generally lower than for the

abundance of all birds (either breeding or foraging), suggesting that factors others than those included in models influence the distribution of territories of open-land birds in our study areas. Recent work has demonstrated that history of land-uses (Kahlert et al., 2007), regional grazing regimes (Reino et al., 2010), hunting activities (Casas et al., 2009) or local levels of human disturbance, both present (López-Jamar et al., 2011) and also past in the case of species showing high site fidelity (Alonso et al., 2004), would additionally affect the distribution and abundance of open-land birds. Lack of replication precludes any meaningful analysis of the likely causes of the differences among regions found in this study. Further work on spatial variation in the effects of farmland management on bird conservation would hence require proper regional replications in their design to address causes of regional effects. Anyway, it was clear that the effectiveness of AES for preserving farmland birds was limited by factors acting at wider spatial and temporal scales, which should be taken into account in their design, application and evaluation.

5. Conclusions

Our results highlight the need to take into account the scale of application of conservation measures for farmland birds even when the focus is on specific guilds. Interestingly, effects at different spatial scales and body sizes differed in strength but not in sign, so that positive effects of farmland extensification detected at a given scale or for a given bird size simply vanished at larger scales or for larger birds at the same scale. This was the case for positive effects on small and medium-sized birds of field-scale extensification, which were not found for large birds. The same was true for positive effects of increased length of natural boundaries around fields. These differentiated, but not contrasting, responses across scales and size groups were presumably due to size-related changes in the scale of perception of agricultural landscapes, rather than to differences in specific habitat requirements, and allow for an integrative conservation strategy including a wide range of farmland management options at nested spatial scales. This was not usually the case when comparing relative responses of birds belonging to different guilds, as positive effects for a given guild at a given scale may turn out to be negative for other guilds due to different, and conflicting, habitat requirements (Batáry et al., 2007; Díaz and Tellería, 1994; Díaz et al., 1998; Gabriel et al., 2010).

Species composition and specialization of farmland bird communities should be considered in a regional context in order to identify conservation priorities and habitat requirements of target groups (Filippi-Codaccioni et al., 2010). In addition, we have shown how open-land birds mostly respond to factors acting at larger spatial scales than those at which AES are applied, even more if we consider the largest and most endangered open-land birds. Hence, conservation policies should adopt a multi-scale approach (Benton et al., 2003, Billeter et al., 2008, Concepción and Díaz, 2010; Concepción et al., 2008; Gabriel et al., 2010) focused on the maintenance of agricultural landscapes able to satisfy habitat requirements of target birds, especially those with wider landscape perception. In this new multi-scale strategy landscape aspects can be tackled through cross-compliance, wide entry level schemes or high nature value farmland programs (Concepción et al., 2008), and be combined with field-scale measures such as AES directed to enhance field conditions related to specific bird requirements. Further research on the nature and magnitude of regional-scale processes are especially needed. Meanwhile, the main goal should be to preserve the extensive agricultural landscapes now occupied by endangered farmland birds, by developing new financial incentives for farmers to maintain rather than to change the already extensive management of their farms. Development of further extensification measures through AES should be subsidiary to measures directed to combat landscape- and regional-scale processes that influence negatively farmland birds.

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Table 1. Summary of management prescriptions and their aims included in the AES applied in the three study areas, which were directed to the protection steppe birds in extensively managed cereal fields in Spain (Kleijn et al., 2006; Llusía and Oñate, 2005).

<i>AES prescriptions</i>	<i>Prescription aims</i>
Maximum annual fertilizer applications 60 kg N/ha	Increased food availability in crops, as well as reduced bird mortality through avoiding early crop growth and harvesting
Maximum pesticide applications 1.5 kg/ha (AAA-type)	Increased food availability by increasing populations of invertebrates and weeds on fields
No agricultural activities between 1 April and 31 May, 15 April to 25 June or 15 April to 10 July depending on area	Reduced bird mortality through avoiding farming practices during the breeding season
No plough of stubble until 1 August or fallow until 15 October if the fields are to be cultivated	Increased food availability harbored by stubbles and fallows (seeds, weeds and invertebrates)
Keep stubble until 1 February or 1 March, depending on area, if the fields are to be left in fallow	Increased food availability harbored by stubbles (seeds, weeds and invertebrates)
No use of dressed seeds	Reduced bird mortality by avoiding bird poisoning
No burning of fallow vegetation	Increased food availability harbored by fallows (seeds, weeds and invertebrates)
Strips covering 3% of the fields are left unploughed	Increased food availability, as well as reduced bird mortality by providing nesting and sheltering habitats

Table 2. Total number of open-land bird species found in study fields (Abundance) both foraging and breeding (Total birds) and only breeding (No. territories), classified by body mass groups (small: < 50 g; medium: 50 – 500 g; large: > 500 g) and regional threat status (VU: vulnerable; IE: special interest; -: not endangered).

Body size group	Species	Threat status	Abundance	
			Total birds	No. territories
Small open-land birds	<i>Melanocorypha calandra</i>	IE	227	56
	<i>Callandrela brachydactyla</i>	IE	6	1
	<i>Galerida cristata</i>	IE	49	9
	<i>Galerida theklae</i>	IE	107	29
	<i>Lullula arborea</i>	IE	3	1
	<i>Oenanthe hispanica</i>	IE	1	1
	<i>Cisticola juncidis</i>	IE	87	25
	<i>Miliaria calandra</i>	IE	441	105
Medium open-land birds	<i>Anas platyrhynchos</i>	-	8	1
	<i>Alectoris rufa</i>	-	95	22
	<i>Coturnix coturnix</i>	-	57	29
	<i>Burhinus oedinenus</i>	IE	4	3
	<i>Upupa epops</i>	IE	4	0
Large open-land birds	<i>Circus aeruginosus</i>	VU	15	1
	<i>Circus cyaneus</i>	VU	15	2
	<i>Circus pygargus</i>	VU	8	0
	<i>Tetrax tetrax</i>	VU	38	24
	<i>Otis tarda</i>	VU	42	10
	<i>Asio flammeus</i>	VU	4	1

Table 3. Results of generalized linear mixed models (GLMM) for the effects of field-scale traits (application of AES, plant species richness and abundance of grasshoppers and crickets), landscape features (size of study fields, and length of semi-natural boundaries and proportion of cropped area within 500-m buffer around study fields) and study area on the species richness and the abundance of small, medium-sized and large open-land birds for both all (either nesting or foraging) and territory-holding birds.

		Field-scale traits			Landscape-scale traits			Study area	Model % D	Model AICc
		AES	Plant species richness	Grasshopper and cricket abundance	Field size (ha)	Length of semi-natural boundaries (m)	Cropped area (%)			
		d.f.=1	d.f.=1	d.f.=1	d.f.=1	d.f.=1	d.f.=1	d.f.=2		
Small birds										
Richness	All birds	-	-	-	-	(+) 7.25**	(+) 7.30**	-	9.24%	123.07
	Territory-holding	-	(+) 4.27*	-	-	(+) 4.45*	(+) 5.07*	-	12.77%	114.42
Abundance	All birds	(+) 21.69***	-	-	-	(+) 5.70*	(+) 26.25***	63.32***	29.81%	292.93
	Territory-holding	(+) 9.96**	-	-	-	-	-	36.67***	22.72%	169.95
Medium-sized birds										
Richness	All birds	-	-	-	-	-	-	-	-	89.37
	Territory-holding	-	-	-	-	-	-	-	-	85.83
Abundance	All birds	-	-	-	(-) 11.40***	(+) 5.56*	-	19.03***	21.30%	159.28
	Territory-holding	-	(+) 7.49**	-	-	-	-	-	7.04%	103.25
Large birds										
Richness	All birds	-	-	-	-	-	-	16.08***	24.46%	81.44
	Territory-holding	-	-	-	-	-	-	9.75**	16.81%	65.06
Abundance	All birds	-	-	-	-	-	(+) 10.28**	21.06***	21.17%	126.19
	Territory-holding	-	-	-	-	-	-	13.38**	17.76%	68.86

Significance levels: *** P < 0.001; ** P < 0.01; * P < 0.05

^a Sign of effects (+/-) and Chi-square estimates are given for each response variable included within best fitted models. Percentage of deviance (% D) accounted for by the best models (as compared with the null model) and the values of the Akaike's information criterion corrected for small sample sizes (AICc) are also given.

Figure 1. Relative contribution (%) of within-field (black), landscape (grey) and regional (stripped) traits to deviance reduction accounted for the best fitted models for the species richness and the abundance of all and territory-holding open-land birds of each body size group (small, medium and large). Open: unexplained deviance.

Open-land birds: **Small** **Medium** **Large**

Species richness

All birds

Territory-holding birds

Abundance

All birds

Territory-holding birds