LETTER

Mixed Effects of Long-Term Conservation Investment in Natura 2000 Farmland

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Abstract

Evaluating the effectiveness of conservation funding is crucial for correct allocation of limited resources. Here we used bird monitoring data to assess the effects of long-term conservation investment in a Natura 2000 (N2000) bird protection area (PA), which during two decades benefited from protection regulations, conservation projects, and agri-environment schemes. Variation between 1995–1997 and 2010–2012 in richness and abundance of flagship (*Otis tarda*, *Tetrax tetrax*, and *Falco naumanni*) and specialized fallow field species were more favorable (i.e., increased more or declined less) inside the PA than in a nearby control area. However, the reverse was found for total bird species, farmland, ground-nesting and steppe species, species associated to ploughed fields, and species of European conservation concern. Enhancing the effectiveness of conservation investment in N2000 farmland may require a greater focus on the wider biodiversity alongside that currently devoted to flagship species, as well as improved matching between conservation and agricultural policies.

Introduction

The Natura 2000 (N2000) network comprises Special Protection Areas (SPA; Directive 79/409/EEC) and Special Areas of Conservation (Directive 92/43/EEC), and is the centerpiece of European Union (EU) nature and biodiversity policy (EC 2013). Most N2000 land is privately owned, consequently establishing and managing Protection Areas (PA) involves considerable conservation investment, part of which has been supported by EU financing mechanisms (EC 2013). The LIFE-Nature programme (LIFE) is one the main schemes, funding best practice and demonstration projects targeting highly threatened species and habitats (EC 2010). Agri-environment schemes (AES) are also key mechanisms providing funds for farmers to promote conservation on farmland under the Common Agriculture Policy (CAP) (Stoate *et al.* 2009). AES are particularly relevant because agriculture is the most important economic activity within European PA (EEA 2006), and extensive farmland supports many species of conservation concern (BirdLife International 2004; Kleijn *et al*. 2011). N2000 has thus major costs to society, either directly through funding mechanisms, or indirectly through eventual opportunity costs of foregone food production and economic activities (Gantioler *et al*. 2010). Evaluating the effectiveness of conservation investments is thus considered a high priority (Kleijn *et al*. 2011; Hochkirch *et al*. 2013).

The effectiveness of EU conservation investments in N2000 is poorly understood, because studies are scarce, and they tend to be geographically biased, short-term, and rarely consider interactions between various protection and funding schemes. For instance, although protection regulations in association with long-term funding should yield positive conservation outcomes in N2000, confirmative quantitative data is generally lacking (Hochkirch *et al*. 2013). LIFE seems to be one of the most effective EU conservation investments (EC 2010), but only a few long-term studies have demonstrated positive population trends of the targeted species (Pinto *et al*. 2005; Catry *et al*. 2009; Bretagnolle *et al*. 2011). Furthermore, these studies have focused on single species, and so it is uncertain whether there were wider benefits on N2000 biodiversity (Devictor *et al*. 2007). In contrast, evaluations of AES included from single species to community level studies, suggesting that they often have null or minor positive effects on biodiversity (Kleijn *et al*. 2011; Concepción *et al*. 2012). However, most studies have been short-term, focusing primarily on central and northern European regions, and not considering specifically the application of AES within N2000 (Batáry *et al*. 2011; Tryjanowski *et al*. 2011). Clearly, further information is needed on the effectiveness of long-term conservation investment in N2000, particularly where there is a combination of protection regulations, LIFE and AES, which might be expected to yield strongly positive biodiversity conservation outcomes.

Here, we provide a case study on the effectiveness of long-term conservation investment in N2000. We focused on a SPA that is representative of Iberian cereal steppes, which hold internationally important populations of bird species of conservation concern (BirdLife International 2004). Since 1993, the SPA has benefited from investments specifically targeted at bird conservation, including: (1) protection regulations restricting activities such as afforestation, expansion of perennial crops (e.g., olive groves), and building of irrigation infrastructures; (2) LIFE targeting flagship species such as *Otis tarda*, *Tetrax tetrax* and *Falco naumanni*; (3) AES designed to maintain agricultural practices beneficial to steppe birds; and (4) concentration of research projects designed to inform conservation management (Table S1). Specifically, we compared breeding bird assemblage trends in the SPA and in a nearby control area, using data collected in 1995–1997 and 2010–2012. We expected that trends would be most favorable (i.e., more positive or less negative) inside the SPA for: (1) overall species richness and abundance (Batáry *et al*. 2011); (2) richness and abundance of farmland species (Guerrero *et al*. 2011), particularly of ground-nesting (Bas *et al*. 2009) and steppe (Stoate *et al*. 2000) specialists; (3) richness and abundance of groups of species associated with each element of the traditional farmland mosaic (i.e., fallow, cereal, and ploughed fields); and (4) richness and abundance of Species of European Conservation Concern (SPEC), and of flagship species that were the main targets of conservation investment (Catry *et al*. 2009; Bretagnolle *et al*. 2011). Finally, we expected that (5) farmland bird assemblage composition would be increasingly dominated by the steppe specialists. Our study has implications for the design of effective AES and other schemes funding conservation on farmland, which are of general relevance for biodiversity conservation both in Europe and elsewhere (Attwood *et al*. 2009; Kleijn *et al*. 2011).

Methods

Study area

The study was conducted in Portugal, in the Castro Verde SPA and in a control area without conservation investment (Figure 1). The landscape is gently undulating (100–300 m a.s.l.), and climate is Mediterranean, with hot summers, mild winters, and >75% of annual rainfall in October–March. The SPA was dominated for decades by traditional rotation of dry cereals and fallows typically grazed by sheep (Delgado & Moreira 2000), but permanent pastures and cattle stocking increased in recent years, along with declines in cereals, fallows, and sheep stocking (Table S2). The control was selected because it was the most comparable farmland area close to the SPA (ca. 10 km), showing overall similarities in dominant land uses at the beginning of the study, though it had smaller farms, less fallow land and more irrigable area (Table S2). In recent years, perennial crops (mainly olive groves) increased at the expenses of cereals (Table S2).

Bird data

Birds were sampled using a network of transects set in 1995 (Stoate *et al*. 2000). Specifically, a 1-km grid was overlaid on the study area, and grid intersections were selected randomly both within the SPA (46) and the

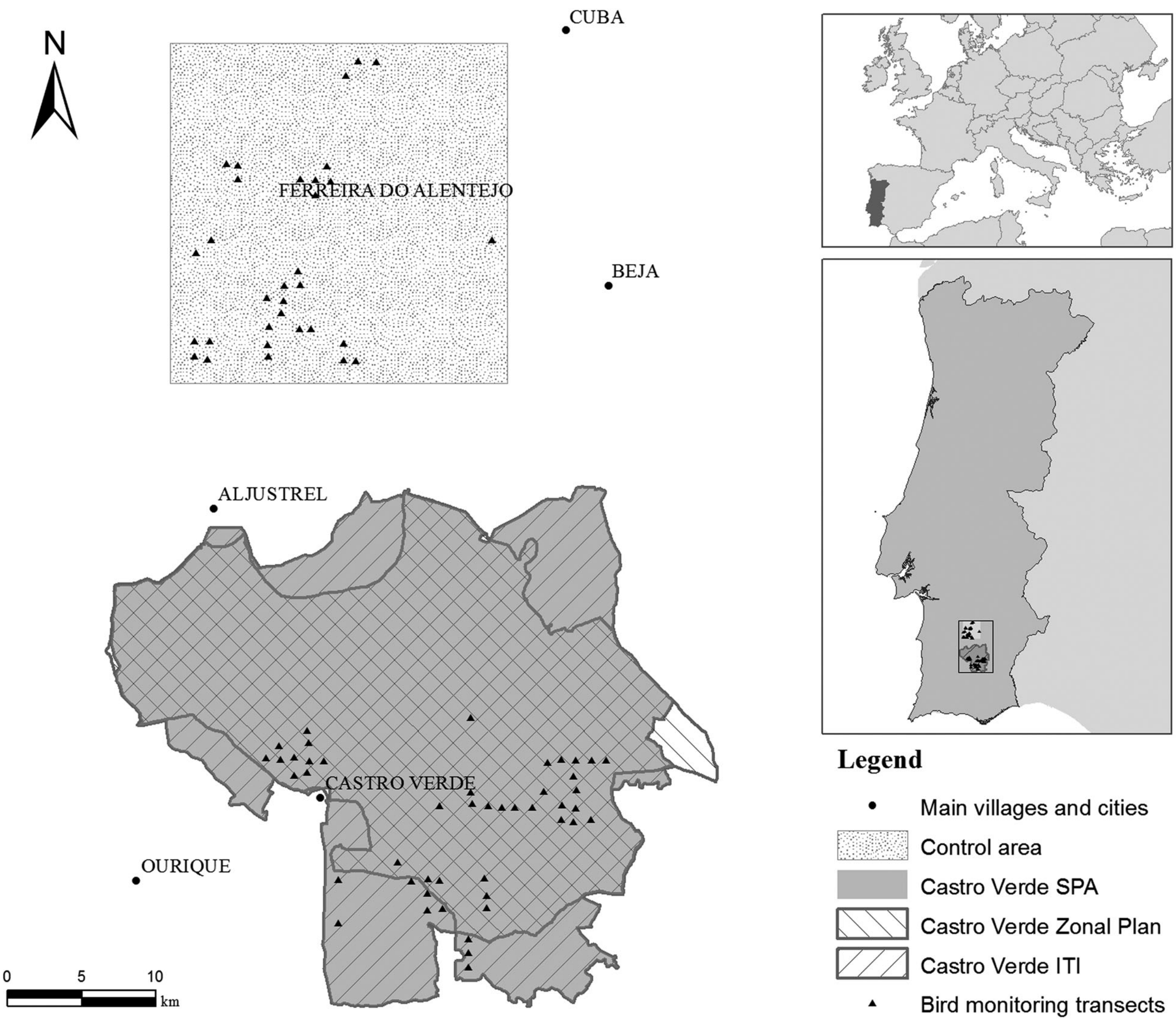

Figure 1 Location of the study area in southern Portugal, showing transects sampled for breeding birds within the Castro Verde SPA ($n = 46$) and the nearby control area ($n = 32$). Areas of implementation of the targeted agri-environment schemes designed for steppe birds conservation are also shown: the Castro Verde Zonal Plan (1995–2006) and the Integrated Territorial Intervention (ITI, 2007–2013).

control (32). One 250-m transect following a random bearing started at each grid intersection. Birds were counted annually once in each transect in April–May, in 1995–1997 and 2010–2012. Occasionally, some transects could not be counted in a given year due to logistic constraints (counts per transect = 5.7 ± 0.6 SD; Table S4). Transects were walked in early morning and late afternoon, and birds seen or heard within 250-m bands were identified and counted. A large searching radius was used to increase detection rate of shy species such as bustards. Although this may have contributed to underestimate relative abundance of small songbirds with low detectability at far distance, this should not have introduced any serious bias, because detectability was high in open farmland habitats, the procedure was consistent across years and sampling areas, and we were interested in temporal trends rather than on relative abundances at any particular time. Aquatic birds were excluded because they are unlikely to respond directly to farmland management and they were inadequately sampled by our approach.

Bird species were categorized to aid interpretation of ecological effects (Table S4). We considered groups reflecting the degree of specialization in open farmland habitats that were the focus of conservation investment: (1) farmland—species associated with all farmland

Table 1 Fixed component of the alternative GLMM candidate models used for model inference, and corresponding ecological effects. SC = SPA versus control area; BA = 1995–97 versus 2010–2012

Alternative models	Ecological effects
H_1 $g_1 = \beta_0$	No effects (null model)
H_2 $g_2 = \beta_0 + \beta_1$ (SC)	Farmland type
H_3 $g_3 = \beta_0 + \beta_1$ (BA)	Period
H_4 $g_4 = \beta_0 + \beta_1$ (SC) $+ \beta_2$ (BA)	Farmland type and period
H_5 $g_5 = \beta_0 + \beta_1$ (SC) $+ \beta_2$ (BA) $+ \beta_3$ (SC $*$ BA)	Farmland type, period and interaction effects (full model)

habitat types (e.g., arable fields, perennial crops, hedgerows); (2) ground-nesting—species nesting on the ground; and (3) steppe—species that are rare or absent outside open grassland habitats. Steppe birds were further grouped according to their associations with elements of the traditional farmland mosaic (i.e., fallow, cereal and ploughed fields; Delgado & Moreira 2000), aiming to identify possible changes reflecting fine modifications in agricultural practices. A group of species with unfavorable conservation status in Europe (SPEC 1–3; BirdLife International 2004) was used to estimate the overall effects on species of conservation concern. Finally, we used a group of flagship species because they are globally threatened and they were the main targets of conservation investment (Table S1).

Analyses

We tested the general hypothesis that temporal bird trends within the SPA were more favorable (i.e., more positive or less negative) than in the control, using a procedure akin to a BACI (Before–After–Control–Impact) design with multiple sites and years (Smith 2006). We modeled species richness (number of species per transect) and abundance (number of birds per transect) against farmland type (SPA vs. control), sampling period (1995–1997 vs. 2010–2012), and their interaction (Table 1). The main interest was on the interaction term, which indicated whether the trend observed in the SPA was above (positive coefficient) or below (negative coefficient) that expected from the trend observed in the control.

Modeling was based on zero-inflated models with negative binomial errors, thereby accounting for excess of zeros and overdispersion (Zuur *et al*. 2009). Generalized linear mixed models (GLMMs) were used to account for lack of independence among samples, treating transects and sampling year as random effects (Pinheiro & Bates 2000). Model building was based on the information theoretic approach, and inference was based on model averaging (Burnham & Anderson 2002). For each dependent variable we calculated: (1) model probabilities (w_i) for all five candidate models (Table 1), based on AIC; (2) model average of each coefficient among models; and (3) 95% confidence intervals (CI) for each model averaged coefficient from unconditional variances (Burnham & Anderson 2002). Dominant gradients in farmland bird assemblage composition were extracted using principal component analysis (PCA) on the bird abundance data for all transects, excluding species with <20 overall occurrences. PC scores were then related to explanatory variables as in previous analyses, using GLMMs with Gaussian errors.

Because the categorization of bird assemblages in many groups may cause spurious relationships, we used a permutation approach to estimate the likelihood of results arising by chance (Petchey & Gaston 2006). Specifically, we compared the coefficient of the interaction term estimated for each species group with the frequency distribution of coefficients estimated using random groups of species (see Table S7 for methodological details). All analyses were performed using packages glmmADMB ("glmmadmb"), lme4 ("glmer"), bbmle ("AIC") and vegan ("prcomp") in R 2.15.2 (R Development Core Team 2012).

Results

Trends in species richness and abundance

Species richness and abundances were generally higher in the SPA than in the control, and they were higher in 2010–2012 than in 1995–1997 (Figures 2 and 3, Table S5). In most cases there was strong support for interaction effects between farmland type and sampling period, suggesting that temporal bird trends differed between the SPA and the control (Figure 4, Table S6). Contrary to our expectation, however, the sign of the interaction coefficient was negative in most cases, suggesting that changes in the SPA were less favorable than expected from corresponding trends in the control (Figure 4, Table S6). This effect was particularly marked for overall species richness, with the highest values found in the SPA in 1995–1997, and in the control in 2010–2012 (Figure 2). Tendencies were less negative for farmland, ground-nesting, and steppe species, along with increasing specialization in open farmland habitats (Figure 4), and this effect was moderately supported by permutation tests (percentiles: 79.4–90.2%; Table S7). Species associated with ploughed fields had much less favorable trends inside the SPA than in the control area (Figure 4), with interaction coefficients being more negative than expected for random groups of steppe birds (percentiles:

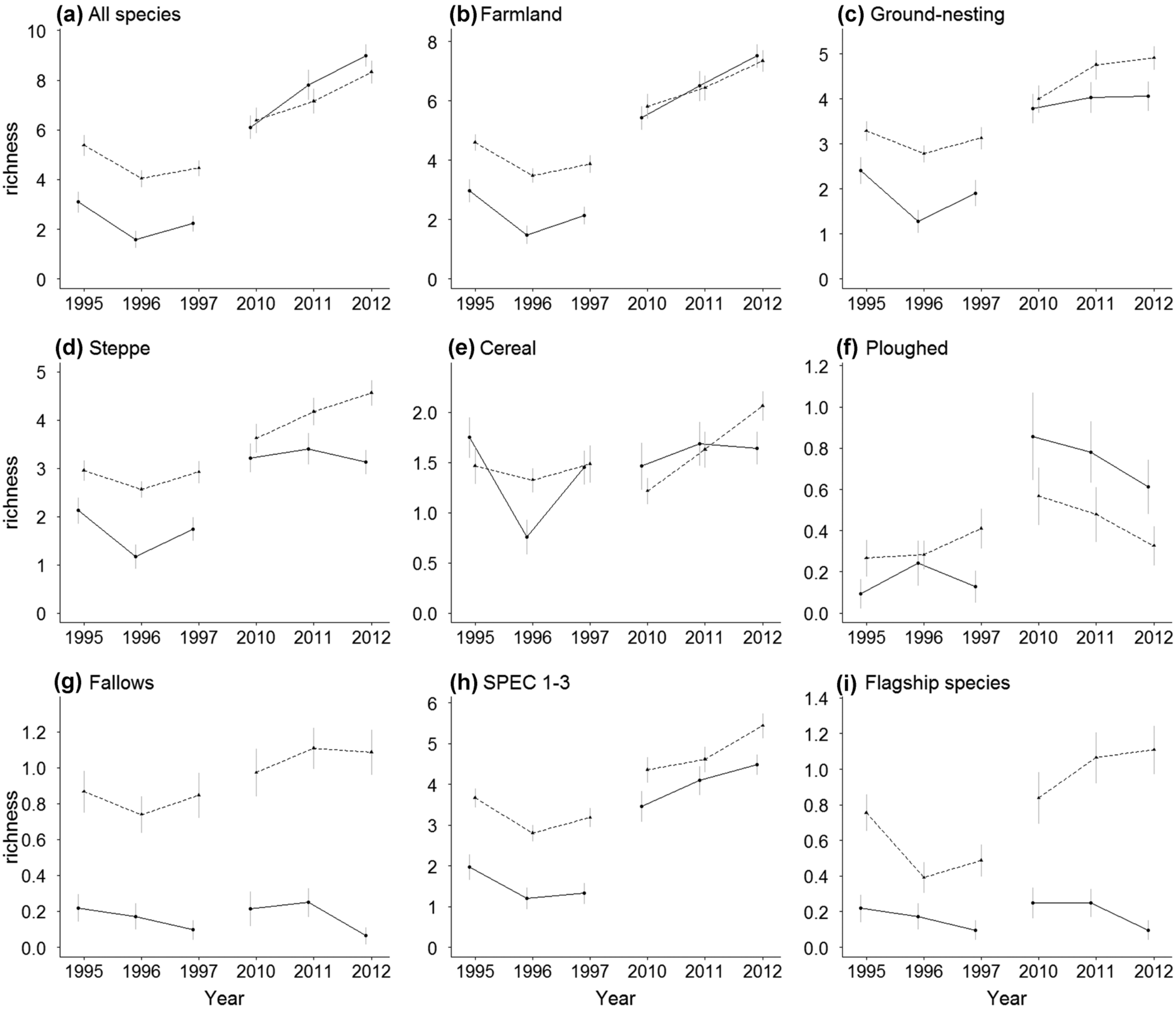

Figure 2 Temporal trends in bird species richness (mean ± standard error) within the Castro Verde SPA (dotted lines) and the control area (full lines).

8.8–10.5%; Table S7). Conversely, effects on species associated with fallows were positive (Figure 4), with coefficients larger than that of random steppe groups (percentiles: 78.1–90.5%; Table S7). No effects were found for species associated with cereal fields (Figure 4; Table S7).

Species of conservation concern (SPEC) had less favorable trends in the SPA than in the control (Figure 4), though the interaction coefficients tended to be less negative than that of random groups of species (percentiles: 76.3–79.1%; Table S7). Conversely, the effect on flagship species was positive (Figure 4), with interaction coefficients more positive than expected for random sets of SPEC (percentiles: 89.0–95.2%; Table S7).

Trends in bird assemblages

Assemblage composition in the SPA and the control diverged over time (Table S8). Variation in the control was most pronounced along PC1 (Figure 5), reflecting increasing dominance by generalist farmland species (e.g., *Sturnus unicolor*, *Saxicola torquatus*, *Merops apiaster*, *Streptopelia decaocto*); variation along PC2 reflected increasing dominance of species associated with ploughed fields (e.g., *Oenanthe hispanica*, *Anthus campestris*, *Calandrella brachydactyla*). Assemblage composition in the SPA was relatively more stable, although there was a tendency for increasing dominance of species associated with cereal fields (e.g., *Cisticola juncidis*, *Emberiza calandra*, *Coturnix*

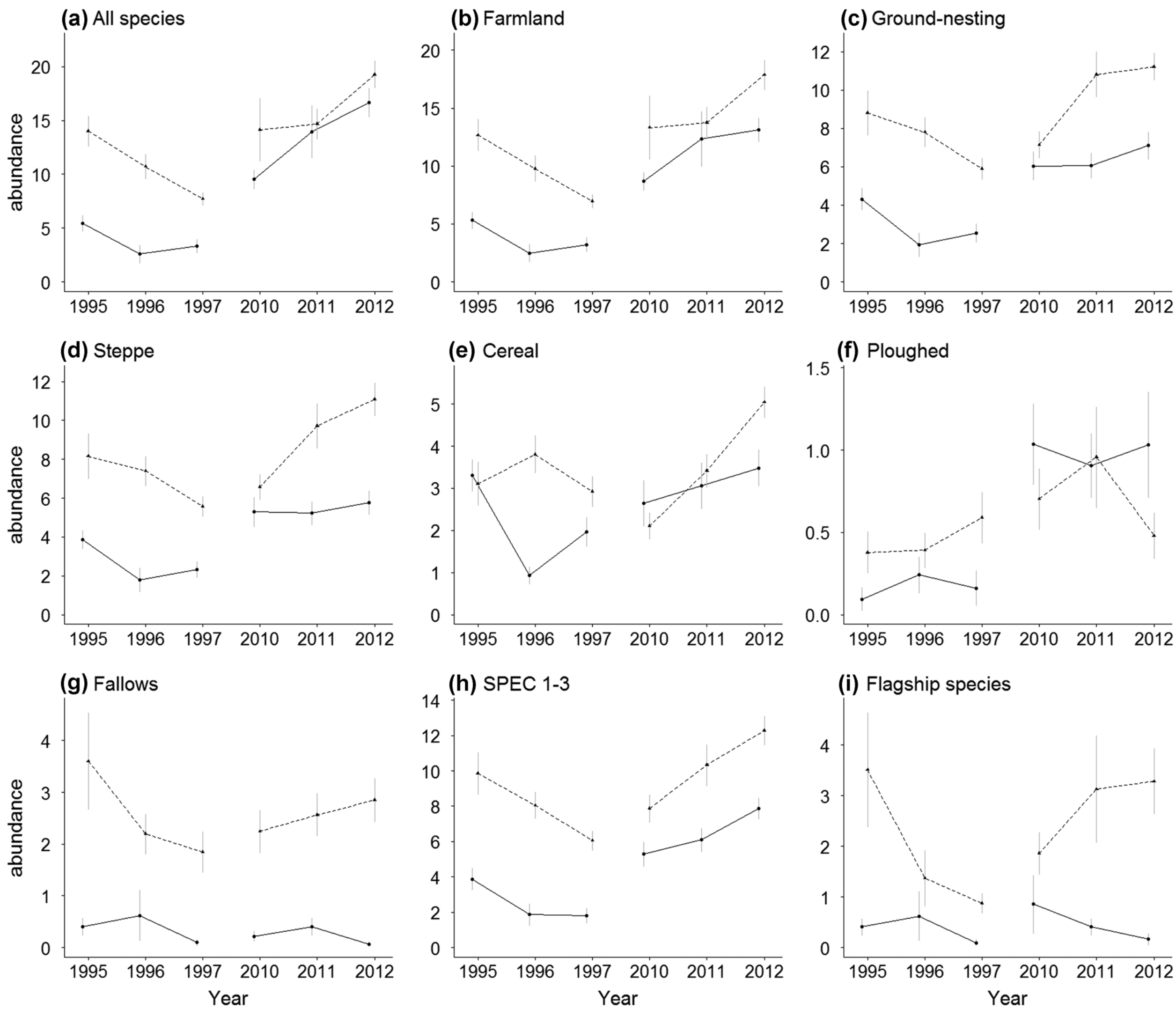

Figure 3 Temporal trends in bird abundance (mean ± standard error) within the Castro Verde SPA (dotted lines) and the control area (full lines).

coturnix, Circus pygargus), and a decline in ploughed field species (Figure 5).

Discussion

Our study showed mixed effects of long-term conservation investment in N2000 farmland. We found positive effects on flagship species, and on species associated with fallows, which were the main targets of conservation investment. In contrast, temporal trends in the control area appeared most favorable for the overall bird assemblage, including the farmland, ground-nesting, and steppe groups of species, and even the Species of European Conservation Concern (SPEC). These patterns seem surprising, because the studied SPA benefited during two decades from protection regulations, LIFE, and AES, whereas the control was under agriculture intensification and did not receive conservation-oriented investments. Interpretation of these results, however, requires due consideration of a number of factors, including potential limitations of the study, shortcomings of general metrics used to judge conservation success, changes in land use (Table S2), and the focus of conservation on a few flagship species (Table S1).

Variation in bird counting skills is unlikely to have affected the patterns observed, because bird detectability in open farmland is high, observers were experienced, and most observers counted birds in both the SPA and the control (98.2% of transects, Table S3). Selection of

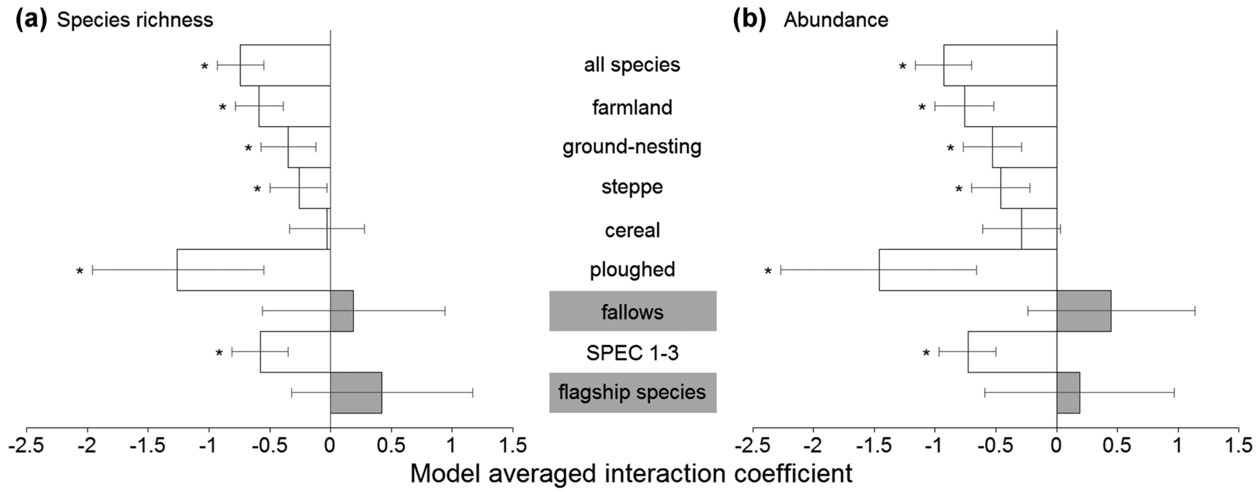

Figure 4 Estimated effects of long-term conservation investment as assessed by the interaction coefficients of models relating bird (a) species richness and (b) abundance to farmland type (SPA vs. control) and sampling period (1995–1997 vs. 2010–2012). Positive coefficients are shown as shaded bars and suggest that bird trends within the SPA were more favorable (i.e., increased more or declined less) than in the control area. Negative coefficients are shown as open bars and suggest the opposite effect. Error bars represent 95% confidence intervals. *Model probability (w_i) for each model with the interaction term (full model) ≥0.8.

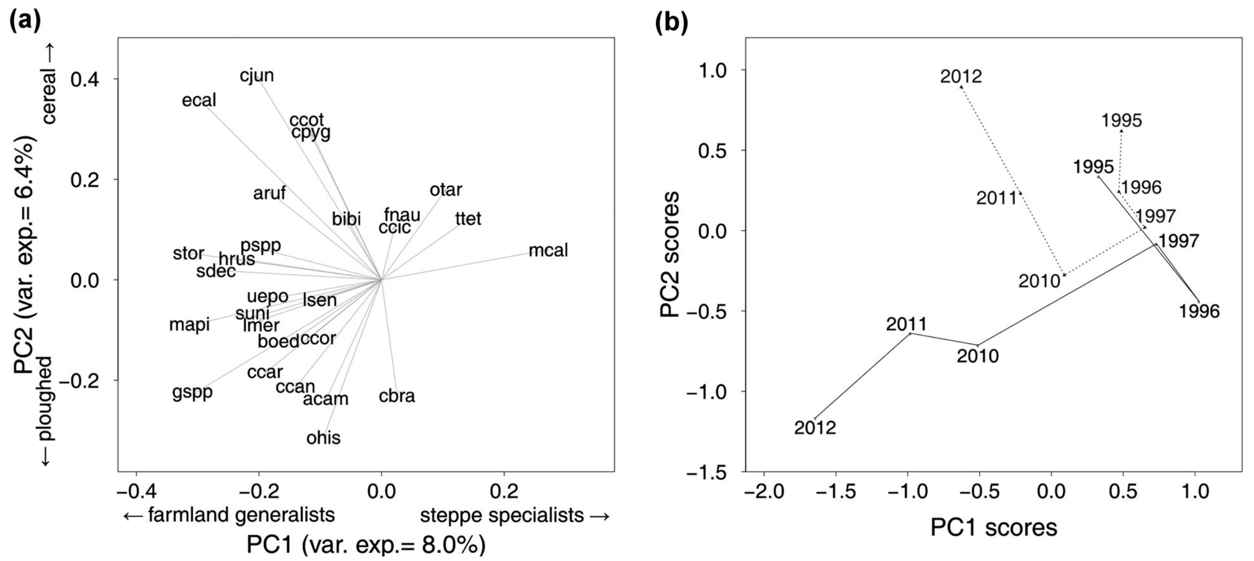

Figure 5 Biplots of a Principal Components Analysis of bird abundances in transects sampled in the Castro Verde SPA and in a control area, in 1995–1997 and 2010–2012: (a) projection of the species, showing the gradient from steppe specialists to farmland generalists (PC1), and from ploughed to cereal field specialists (PC2); (b) projection of annual mean site scores, reflecting the dominant trends of assemblage variation in the SPA (dotted lines) and the control area (full lines). Species abbreviations are provided in Table S4.

two areas as similar as possible (Table S2) should have minimized the problem of initial landscape characteristics driving differences in bird trends (Concepción *et al.* 2012). In fact, bird assemblages observed at study outset were similar, diverging only afterwards, probably due to processes occurring during the study and not as much due to differences in initial landscape conditions. Results might also reflect unusual idiosyncrasies of the study areas, such as poor SPA management, or the emergence of conservation-oriented farming in the control. This is also unlikely, because the SPA was comparable to other Iberian cereal steppes and the most threatened species showed largely favorable trends (Pinto *et al.* 2005; Catry *et al.* 2009; Moreira *et al.* 2012; this study), while the control was a typical irrigated area undergoing agricultural intensification (Stoate *et al.* 2000). Also, building of a highway in the middle of the study period might have influenced bird trends (López-Jamar *et al.* 2011), but this is unlikely because it affected both the SPA and the control, and there were no measurable effects on very sensitive species such as *Otis tarda*. Finally, it is conceivable that sometime during the study period bird species richness and abundance reached saturation in the SPA, causing spillover to the nearby control area. Discarding this possibility would require longer time series and detailed population data, but it is worth noting that spillover would imply increasing assemblage homogenization, whereas we observed divergence over time.

Although general biodiversity measures are often used to evaluate conservation investments (e.g., Bátary *et al.* 2011; Concepción *et al.* 2012), it is possible that metrics such as overall, farmland, and even SPEC species richness and abundance are misleading indicators of conservation success in Iberian cereal steppes. Here, these metrics may increase due to shrub encroachment, afforestation, and expansion of perennial crops (Diaz *et al.* 1998; Reino *et al.* 2009, 2010; Santana *et al.* 2012), but these processes are detrimental for the relatively species-poor but highly specialized assemblage of steppe birds that include several species of high conservation concern (Suárez *et al.* 1997; Delgado & Moreira 2000; Concepción & Díaz 2010; Reino *et al.* 2010). This probably helps to explain the most favorable trends observed in the control area, where the progressive introduction of olive groves in a landscape dominated by pastures and annual crops is likely to have increased habitat heterogeneity, and thus enhanced conditions for a wider range of generalist species (Benton *et al.* 2003). These results reinforce the point that in some cases low-intensity farmland supports poorer but more specialized bird assemblages than intensive farmland (Doxa *et al.* 2010), suggesting that evaluations of conservation investment should consider indicators reflecting assemblage specialization (Filippi-Codaccioni *et al.* 2010). Overall biodiversity measures may remain useful, however, where maintaining landscape heterogeneity and high species richness are important conservation goals (e.g., Tryjanowski *et al.* 2011).

The less favorable trends observed in the SPA for the specialized ground-nesting and steppe bird species may indicate limited conservation success, probably reflecting recent land use changes. Although AES were designed to favor the traditional farming system, the CAP reform of 2003 provided economic incentives promoting a shift to specialized livestock production (Ribeiro *et al.* 2014). There was thus a progressive increase of pasture land, at the expenses of cereal and ploughed fields, which was far more marked in the SPA than in the control (Table S2). The expansion of pastures should have benefited species typically associated with fallows, because the two habitats may be structurally similar (Suárez *et al.* 1997; Delgado & Moreira 2000). No effects were found for species associated to cereal fields, because declines in this habitat were similar in the SPA and the control (Table S2). In contrast, species associated to ploughed fields declined in the SPA due to reductions in cereal cultivation, but they increased in the control because recently planted olive groves have bare ground akin to ploughed fields. Results suggest that a mosaic of arable crops and pastures may be critical to maintain conditions for steppe birds with contrasting habitat requirements, further supporting the importance of landscape scale factors to promote conservation on farmland (Concepción & Diaz 2010; Concepción *et al.* 2012). Conservation investment appeared unable to preserve such mosaics, probably because livestock specialization driven by CAP was not counterbalanced by adequate regulations or funding schemes.

Conservation investment appeared positive on populations of highly threatened flagship species (*O. tarda*, *T. tetrax*, and *F. naumanni*), supporting the view that targeted efforts combining legal regulations and adequate funding schemes may deliver major conservation benefits (Batáry *et al.* 2011; Bretagnolle *et al.* 2011; Baker *et al.* 2012). Although the effects observed were relatively weak, this was probably a consequence of the generalist sampling design used in here, as other, more directed studies have demonstrated stronger positive effects (Pinto *et al.* 2005; Catry *et al.* 2009; Moreira *et al.* 2012). Positive trends were probably a consequence of targeted LIFE, including the purchase and management of critical areas, and the improvement of breeding and foraging habitats (Pinto *et al.* 2005; Catry *et al.* 2009; Moreira *et al.* 2012). Simultaneously, there were likely benefits from legal regulations preventing afforestation, the conversion to perennial crops, and the expansion of irrigated agriculture, which have caused detrimental changes in landscape composition and structure outside the SPA. This issue may be key, but has not been evaluated properly. The direct effect of AES is uncertain, because they apparently failed to promote the traditional rotational farming system (Ribeiro *et al.* 2014), though they may have contributed to prevent land abandonment (Stoate *et al.* 2009). The contrasting effectiveness observed for flagship species and other steppe birds suggests that investment concentrating on charismatic species does not necessarily lead to the conservation of the overall steppe bird assemblage (Caro 2010).

Conclusions

Our study has some general implications for the design and evaluation of conservation investment on farmland, both in Europe and elsewhere (Attwood *et al.* 2009; Kleijn *et al.* 2011). First, we suggest that general biodiversity measures may be in some circumstances misleading indicators of conservation success. Parameters specifically tailored to reflect the outcome of conservation interventions may thus be needed, focusing for instance on the richness and abundance of groups of species of conservation concern that are specialized in specific habitat types. Second, voluntary schemes such as AES may fail to deliver its expected benefits if they are countered by more attractive economic incentives, thus calling for a better integration of conservation and agricultural policies. Third, focusing investment on flagship species may help the recovery of highly threatened species without wider benefits on less charismatic species of conservation concern, suggesting that more encompassing efforts should be developed. Finally, long-term evaluations of conservation investment are required, in order to monitor and improve the effectiveness of billions of euros needed annually for managing N2000 (Gantioler *et al.* 2010).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1 Summary of key conservation investments made in the Castro Verde Special Protection Area (southern Portugal) between 1993 and 2012.

Table S2 Summary of the land-use changes during the study, using the Portuguese Agricultural Census from 1999 (1995–1997) and 2009 (2010–2012) for the main municipalities of the study area (see Figure 1): Castro Verde (SPA) and Ferreira do Alentejo (Control) (INE 1999, 2009; http://ra09.ine.pt/xportal/xmain?xpid=RA2009&xpgid=ine_ra_publicacoes&xlang=en).

Table S3 Distribution of bird sampling effort (number of transects) and observers across farming type (SPA and Control) and period (1995–1997 and 2010–2012).

Table S4 Mean count per transect ± standard error (minimal and maximum) and percentage of occurrence (Occ) of birds recorded in 78 plots in the Castro Verde Special Protection Area (SPA) and in a control area (Control) (southern Portugal). Species are categorized in terms of habitat specialization (Habitat) and conservation status (SPEC). For each species we indicate the conservation status in Europe (SPEC). Abbreviation (Abbr) is provided for species used in the Principal Components Analysis shown in Figure 5. Flagship species are underlined.

Table S5 Mean richness (number of species per transect) and abundance (number of birds per transect) ± standard error (minimum and maximum) and percentage of occurrence (Occ) of bird categories from 78 plots sampled in the Castro Verde Special Protection Area (SPA) and in a control area (Control) (southern Portugal).

Table S6 Model averaged coefficients (95% confidence intervals) from the five candidate models (Table 1), using a negative binomial family and zero inflation correction ("glmmadmb" function), relating bird species richness and abundance to farmland type (SC; Castro Verde SPA vs. control area), sampling period (BA; 1995–1997 vs. 2010–2012), and an interaction term (SC:BA). Model probabilities (w_i) for each full model are also given.

Table S7 Summary results of permutations tests (10,000 permutations) comparing results obtained with focal and random groups of species. In each case we report the percentile of the interaction coefficient estimated for the focal group in relation to the frequency distribution of coefficients estimated for random groups. Large percentiles (close to 100%) indicate that the coefficient was larger (i.e., more positive or less negative) than it might be expected by chance, whereas small percentiles (close to 0%) indicate that the coefficient was smaller (i.e., more negative or less positive) than it might be expected by chance. Finally, medium percentiles (close to 50%) indicate that coefficient was not different than expected by chance. Random groups were obtained by random sampling (without replacement) of species from a larger species pool, while maintaining the same species richness of the focal group. As groups were built hierarchically (e.g., farmland species were a subset of all species, whereas ground-nesting species were a subset of farmland species), the species pool used in each random sampling respected the same hierarchy. In some cases, random sampling produced sets of species that could not be analyzed using zero inflation models with negative binomial errors (fitted using "glmmadmb" function, Neg. binomial) due to lack of convergence, and so these sets were discarded from analysis. The impact of this option was negligible, because similar analysis with Poisson errors and without zero inflation correction (fitted using "glmer" function, Poisson) produced basically the same results.

Table S8 Model averaged coefficients (95% confidence intervals) of models relating site scores along the first two axis (PC1 and PC2) extracted from a Principal Component Analysis, to farmland type (SC; Castro Verde SPA vs. control area), sampling period (BA; 1995–1997 vs. 2010–2012), and an interaction term (SC:BA). Model probabilities (w_i) for each full model (full model) are also given (see Table 1).

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