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Authors

Santana, Joana
Porto, Miguel
Reino, Luís
et al.

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Using beta diversity to inform agricultural policies and conservation actions on Mediterranean farmland

Joana Santana*[,1,2], Miguel Porto[1,2], Luís Reino[1,2], Francisco Moreira[2,3], Paulo Flores Ribeiro[4], José Lima Santos[4], John T. Rotenberry[5] and Pedro Beja[2,6]

[1]CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-601 Vairão, Portugal; [2]CEABN/InBIO, Centro de Ecologia Aplicada "Professor Baeta Neves", Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal; [3]REN Biodiversity Chair, CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-601 Vairão, Portugal; [4]CEF, Centro de Estudos Florestais, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349–017 Lisboa, Portugal; [5]Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, MN 55108, USA; and [6]Cátedra EDP Biodiversidade, CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-601 Vairão, Portugal

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Summary

1. Spatial variation in species composition (β-diversity) is an important component of farmland biodiversity, which together with local richness (α-diversity) drives the number of species in a region (γ-diversity). However, β-diversity is seldom used to inform conservation, due to limited understanding of its responses to agricultural management, and lack of clear links between β-diversity changes and conservation outcomes.

2. We explored the value of β-diversity to guide conservation on farmland, by quantifying the contribution of bird α- and β-diversity to γ-diversity variation in low- and high-intensity Mediterranean farmland, before (1995–1997) and after (2010–2012) the Common Agricultural Policy reform of 2003. We further related β-diversity to landscape heterogeneity, and assessed the conservation significance of β-diversity changes.

3. In 1995–1997, bird diversity was highest in low-intensity farmland, where it further increased in 2010–2012 due to a strong positive contribution of α-diversity to γ-diversity. In high-intensity farmland, diversity converged over time to much the same values of low-intensity farmland, with strong positive contributions of both α- and β-diversity. These patterns were largely consistent for total, farmland and species of European conservation concern assemblages, and less so for steppe birds.

4. Beta diversity increased with landscape heterogeneity, particularly related to spatial gradients from agricultural to natural habitats in low-intensity farmland, and from annual to permanent crops (olive groves) in high-intensity farmland. The first gradient was associated with the replacement of steppe birds of high conservation concern by more generalist species, while the second was associated with the replacement between species with lower or higher affinity for woodland and shrubland habitats.

5. *Synthesis and applications*. In low-intensity farmland, spatial variation in species composition (β-diversity) was largely stable over time, reflecting a positive conservation outcome related to persistence of landscape heterogeneity patterns required by endangered steppe bird species. In contrast, β-diversity in high-intensity farmland was favoured by increases in landscape heterogeneity driven by olive grove expansion, contributing to enhancement of total bird diversity. Overall, our results stress the value of β-diversity to understand impacts of agricultural policies and conservation actions, but also highlight the need to evaluate β-diversity changes against specific conservation goals.

*Correspondence author. E-mail: joanafsantana@cibio.up.pt

Key-words: agriculture intensification, beta diversity, biodiversity conservation, farmland birds, land-use changes, olive groves, species replacement, species richness difference, steppe birds

Introduction

The effects of human activities on biodiversity are generally assessed by estimating trends in local species richness (alpha diversity, α, *sensu* Whittaker 1960) for particular species assemblages (Newbold *et al.* 2015). However, this metric provides only a partial view of biodiversity change, because the total number of species represented in a region (i.e. gamma diversity, γ) is shaped by both α-diversity and by variation in species composition among sites (beta diversity, β) (Whittaker 1960). Therefore, examining trends in β-diversity may be useful to understand the impacts of anthropogenic drivers whose effects on γ-diversity may not be adequately captured by α-diversity alone (Socolar *et al.* 2016). For instance, land-use changes increasing habitat diversity may increase β-diversity due to species replacement among sites with different habitats (i.e. the replacement component of β-diversity, β_{Repl}; Legendre 2014), and thus increase γ-diversity without necessarily changing α-diversity (Gaston *et al.* 2007; Monnet *et al.* 2014). Alternatively, land-use changes affecting habitat attributes may cause variation in the number of species among sites with different habitat characteristics (i.e. the richness difference component of β-diversity, $\beta_{\mathrm{RichDiff}}$; Legendre 2014), without necessarily affecting β_{Repl}. In this case, the contribution of β-diversity to γ-diversity will likely be relatively small, and local factors affecting α-diversity may be particularly relevant. There is thus a need to consider β-diversity and its components, β_{Repl} and $\beta_{\mathrm{RichDiff}}$, in conservation research to understand biodiversity changes and their underlying ecological mechanisms (Socolar *et al.* 2016; Żmihorski *et al.* 2016).

On farmland, the diversity and spatial arrangement of habitats (i.e. landscape heterogeneity) are widely recognised as key for biodiversity conservation (Benton, Vickery & Wilson 2003; Fahrig *et al.* 2011; but see Báldi & Batáry 2011). Loss of heterogeneity due for instance to crop specialisation, loss of crop rotations, enlargement of fields and loss of non-crop habitats (e.g. woodland patches, scattered trees, hedgerows, and ponds), is a dominant driver of farmland biodiversity declines (e.g. Benton, Vickery & Wilson 2003). As a consequence, agri-environment schemes and other agricultural policies aim to maintain or restore landscape heterogeneity, though their actual biodiversity benefits remain disputed (Stoate *et al.* 2009; Batáry *et al.* 2015). A few studies have used β-diversity to address these issues, providing evidence that β-diversity was lower in intensive than in extensive farmland (Ekroos, Heliölä & Kuussaari 2010; Flohre *et al.* 2011; Karp *et al.* 2012), and in conventional than in organic farms (Gabriel *et al.* 2006; Clough *et al.* 2007), though the patterns observed varied across spatial scales, taxa and functional groups. However, to the best of our knowledge no study has yet evaluated how β-diversity varies through time in response to changes in agricultural policies and conservation actions, though understanding this variation would be relevant for improving agricultural policies, land planning and conservation management prescriptions to reverse farmland biodiversity loss.

Here, we address these issues by quantifying the patterns and correlates of farmland bird diversity during a period of major land-use change. We focused on two contrasting areas in southern Portugal, one of which was a special protection area (SPA) representative of low-intensity farmland and holding internationally important steppe bird populations, while the other was a nearby high-intensity farmland area (Ribeiro *et al.* 2014; Santana *et al.* 2014, 2017a). The study was conducted before (1995–1997) and after (2010–2012) the Common Agricultural Policy (CAP) reform of 2003, which in our area was associated with marked expansions in land uses previously scarce in the region (Ribeiro *et al.* 2014), and with significant increases in α-diversity of breeding birds due primarily to increases in species that benefited from woodland and shrubland habitats and olive groves (Santana *et al.* 2014, 2017a). We hypothesise that these changes should also have affected γ-diversity, both due to the observed increases in α-diversity, and because likely increases in landscape heterogeneity should have contributed to increasing species replacement (β_{Repl}) and thus overall β-diversity. However, we also hypothesise that the effects of heterogeneity on diversity probably varied across species groups, because while some species are favoured by heterogeneity (Fahrig *et al.* 2011), others such as steppe birds are associated with relatively homogeneous landscapes (Báldi & Batáry 2011). To test these ideas, we examined: (i) temporal trends in landscape heterogeneity and the contribution of specific land uses to such trends; (ii) temporal trends in bird diversity and the contribution of α- and β-diversity to γ-diversity; (iii) the relations between β-diversity and landscape heterogeneity; and (iv) the identity of species contributing most to the relations between β-diversity and landscape heterogeneity. Results were used to discuss the value and limitations of β-diversity to inform conservation management on farmland.

Materials and methods

STUDY AREA

The study was conducted in southern Portugal, within a low-intensity farmland area included in the SPA of Castro Verde

(37°41′N, 8°00′W), and within the nearby (about 10-km distant) high-intensity farmland area of Ferreira do Alentejo (38°03′N, 8°06′W) (Fig. 1). The low-intensity area was dominated for decades by a traditional farming system characterised by the rotation of rain-fed cereals and fallows typically grazed by sheep, which provide habitat for steppe bird species of conservation concern (Delgado & Moreira 2000; Santana *et al.* 2014). To preserve this system, a voluntary agri-environment scheme was established in 1995, while legal regulations setting restrictions to afforestation, the development of irrigation infrastructures, and the expansion of permanent crops were established after the creation of the SPA in 1999 (Ribeiro *et al.* 2014). Furthermore, there were conservation projects targeting mainly great bustard *Otis tarda*, little bustard *Tetrax tetrax* and lesser kestrel *Falco naumanni*, which included the purchase and management of critical areas, and improvement of breeding and foraging habitats (Santana *et al.* 2014 and references within). Despite these interventions, over the last decade there were marked shifts from the traditional system towards the specialised production of either cattle or sheep, with declines in cereal and fallow land, and increases in pastures (Ribeiro *et al.* 2014). This probably resulted from the decoupling of payments from production introduced by the CAP reform of 2003 (i.e. farmers were no longer required to maintain production for receiving CAP payments), as arable crops were completely decoupled while sheep and suckler cows remained partially and fully coupled, respectively (Ribeiro *et al.* 2014). The high-intensity farmland contrasted markedly to the SPA, because it had irrigation infrastructures, better soils, and no constraints to crop conversion (Ribeiro *et al.* 2014). At beginning of the study, this farmland area mainly produced irrigated annual crops, but thereafter there was a major shift towards the production of permanent crops (mainly olive groves) (Ribeiro *et al.* 2014).

SAMPLING DESIGN

The study was based on a network of 250-m transects established in 1995, where birds were counted annually in 1995–1997 and 2010–2012, thus covering periods before and after the CAP reform of 2003 and the development of steppe bird conservation programs (Stoate, Araújo & Borralho 2003; Santana *et al.* 2014). These transects were initially designed to evaluate the effects of an agri-environment scheme (Stoate, Araújo & Borralho 2003), with 46 transects set in the SPA and 32 in a nearby high-intensity farmland area (Santana *et al.* 2014). From these, we retained 43 transects in low-intensity and 30 transects in high-intensity farmland that were surveyed in at least 2 years in each period (Santana *et al.* 2017a). Transects followed a random bearing, and they started at grid intersections of a 1-km square grid overlaid on the study area, which were selected based on access constraints and the presence of agricultural land uses (Stoate, Araújo & Borralho 2003).

HABITAT CHARACTERISATION

We characterised the habitats within 250-m buffers (32·12 ha) of each transect using the land cover maps for 1995–1997 and 2010–2012 described in Santana *et al.* (2017a) (Fig. 1). Briefly, maps were produced using digital aerial photographs from 1995 (scale 1 : 40 000), and Bing Aerial images from October 2010 to July 2011, respectively. Mapping was refined with information from a governmental database of agricultural land uses at the parcel scale (Ribeiro *et al.* 2014), using data from 2000 and 2010 to represent crop types in 1995–1997 and 2010–2012, respectively. Using a single land cover map for each study period is reasonable because our land cover categories were not expected to drastically change within each 3-year period. These categories were selected

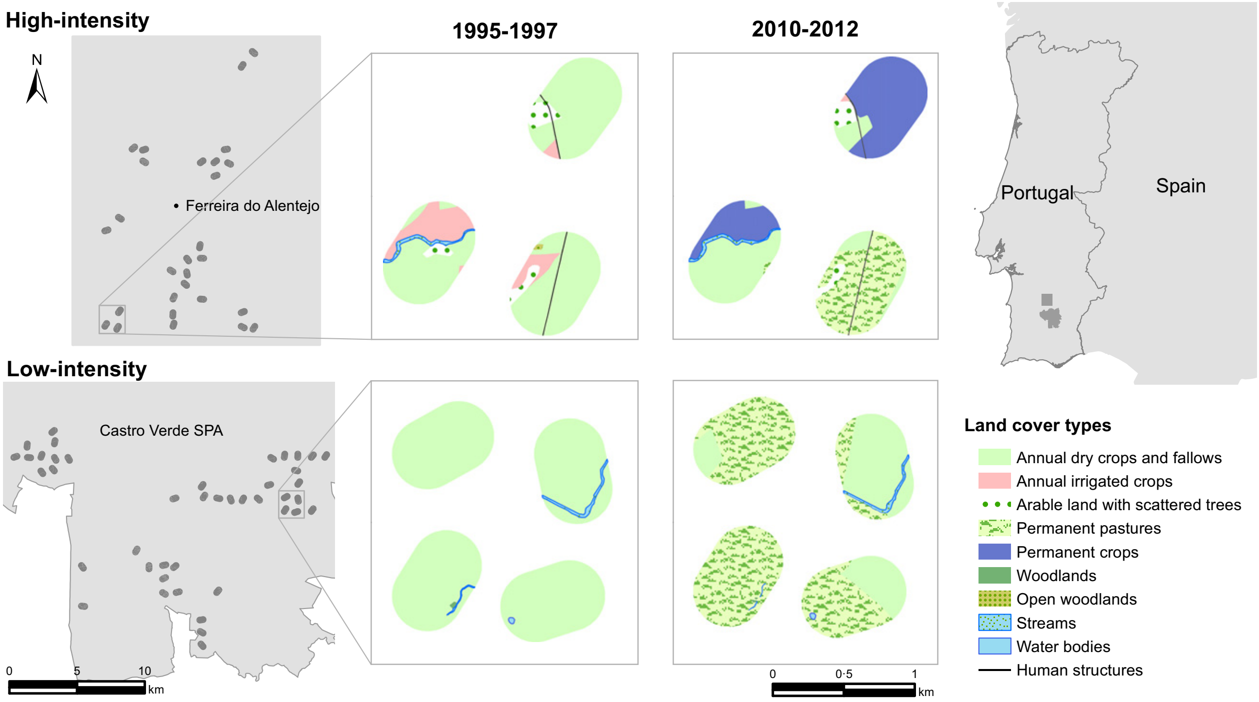


Fig. 1. Location of the study area in Southern Portugal and distribution of the 71 sampling units in the high- and low-intensity farmland areas, with examples of landscape changes from 1995–1997 to 2010–2012. [Colour figure can be viewed at wileyonlinelibrary.com]

to reflect potentially important bird habitats, considering both the natural (woodlands, open woodlands, shrublands, streams and water bodies) and production (annual dry crops and fallows, permanent pastures, annual irrigated crops, arable land with scattered trees and permanent crops) components of the landscape (Santana *et al.* 2017a). We also computed metrics reflecting habitat diversity and configuration (number of different cover types, mean patch size and edge density), which were estimated separately for the natural and the production components, using Fragstats 4.2 (McGarigal & Ene 2013).

LANDSCAPE HETEROGENEITY

Landscape heterogeneity was estimated following the approach described by Anderson, Ellingsen & McArdle (2006), which was previously used in our study area to compare landscape patterns across farming systems (Ribeiro *et al.* 2016a). First, we computed for each farmland area and time period the average dissimilarity in habitat characteristics from individual transects to their group centroid in multivariate space, which is a multivariate dispersion metric that can be interpreted as a measure of overall landscape heterogeneity (Anderson, Ellingsen & McArdle 2006). To avoid inflating the effects of potentially correlated variables, estimates were made using the axes of a principal component analysis on the habitat variables (Habitat PCA) (see below). Second, we estimated dispersion along each independent Habitat PCA axis, to evaluate which habitat gradients contributed the most to overall landscape heterogeneity. Finally, we estimated pairwise landscape heterogeneity as the Euclidean distance between each pair of transects along each Habitat PCA (Anderson, Ellingsen & McArdle 2006), which was used in analyses relating β-diversity metrics to landscape heterogeneity (see below).

BIRD SURVEYS

In each study year, transects were walked in early morning and late afternoon in April–May, and birds species detected within 250-m bands were registered (details in Santana *et al.* 2014). The months of sampling were adjusted to cover the breeding periods of both resident species and trans-Saharan migrants (Table S1, Supporting Information). Before analysis, we pooled species occurrences at each transect within each 3-year period, to minimise potential confounding effects resulting from year-to-year fluctuations in species occurrences unrelated to local habitat conditions, differences in observer skills, and the possibility of missing some species when sampling on a single sampling occasion per year. To aid interpretation of ecological effects, bird species were categorised according to their specialisation in farmland habitats (Santana *et al.* 2014; Table S1): farmland birds – species associated with a range of farmland habitats (e.g. arable fields, permanent crops, hedgerows); and steppe birds – a subset of farmland birds occurring only in open grassland habitats. We also categorised birds with unfavourable conservation status in Europe (SPEC1-3, BirdLife International 2004). Aquatic birds were discarded because they were not adequately sampled (Table S1). Because no birds were observed for some transects in a given period, they were discarded from subsequent analyses, corresponding to three transects for steppe birds, and two transects for the other bird categories.

BIRD DIVERSITY METRICS

The γ-diversity in each farmland area was computed for each 3-year period, while correcting for differences in sampling effort between areas. We used Chao estimator implemented in 'iNEXT' (Hsieh, Ma & Chao 2016) for R 3.2.3 (R Core Team 2016), assuming that sampling was thorough enough so that the landscape heterogeneity was well captured within the sampled sites (Santana *et al.* 2017a). Specifically, we estimated how many species would be observed if sample size was as large in high- as in low-intensity farmland, and computed the 95% confidence intervals of estimates. Sample size-based rarefaction and sample completeness curves were used to evaluate whether our sampling effort was reasonable to estimate species richness.

Estimates of α-diversity were taken from Santana *et al.* (2017a), and they were used here to allow comparisons with spatial and temporal trends in β- and γ-diversity. Total beta diversity (β_{Tot}) was estimated by calculating pairwise dissimilarity in species composition between all pairs of transects within each farmland area and period, using the Jaccard index (Legendre 2014). The index was additively decomposed into two components to identify the dominant process driving compositional change: (i) species replacement (β_{Repl}) – differences in species composition between transects; and (ii) species richness difference ($\beta_{\mathrm{RichDiff}}$) – differences in the number of species between transects (Legendre 2014; see Table S2 for formulation). The different number of transects sampled in each farmland area was unlikely to have effects on pairwise β-diversity metrics because they were based on the average of the differences in species composition between transects. The mean and the range of the distances between transects were similar in high- (mean distance between transects; min–max: 8·6 km; 0·76–22·7 km) and low-intensity farmland (10·4 km; 0·79–23·0 km).

STATISTICAL ANALYSIS

Before analysis, we used the angular transformation on proportional data and the log-transformation on habitat diversity and configuration metrics, to minimise potential problems associated with the unit sum constraint and the undue influence of extreme values. For each farmland area, we then carried out a principal component analyses of habitat variables (Habitat PCA), with varimax rotation on components with eigenvalues >1·0 (Legendre & Legendre 1998), to describe the main habitat gradients and estimate landscape heterogeneity metrics. Land cover types with less than three occurrences were excluded to reduce the possible unduly large influence of rare land-use categories (Legendre & Legendre 1998). We used *t*-tests to evaluate differences between time periods in the mean (habitat patterns) and dispersion (overall landscape heterogeneity) of transect scores along each Habitat PCA axis.

We used multiple linear models to analyse how β_{Tot}, β_{Repl} and $\beta_{\mathrm{RichDiff}}$ varied between time periods [1995–1997 (0) vs. 2010–2012 (1)] and farmland area [high-intensity (0) vs. low-intensity (1)], and whether temporal trends varied between farmland area (interaction term). Under our model parameterisation, positive coefficients for the interaction term indicate that temporal trends in β-diversity metrics were more positive (or less negative) in low-intensity farmland compared to high-intensity farmland. The significance of model coefficients was tested using a permutation approach (Legendre & Legendre 1998), because the underlying data matrix was comprised of pairwise indices that are computed for all combinations of two transects, thereby inflating estimates of parametric significance due to pseudo-replication. Therefore, we compared the coefficients estimated for each model with the frequency distribution of coefficients estimated using 10 000 random permutations of transects among farmland areas, and time periods, but maintaining the original number of transects per area and period.

We used multiple regression on distance matrices (MRM; Lichstein 2007) to model the relationships between pairwise β-diversity metrics and pairwise landscape heterogeneity along each Habitat PCA axis. A separate model was fit for each farmland area and time period, including in each case all principal components and the matrix of geographical distances between the coordinates of transects to account for spatial autocorrelation (Lichstein 2007). We did not use any model selection procedure, because the number of variables was low in relation to the number of observations, and variables were not intercorrelated. Statistical significance of model coefficients was estimated using a permutation procedure with 10 000 permutations (Legendre, Lapointe & Casgrain 1994).

To help explain the observed variations of β-diversity metrics in terms of actual spatial variations in bird assemblage composition (e.g. Legendre, Borcard & Peres-Neto 2005; Tuomisto & Ruokolainen 2006), we used partial constrained correspondence analysis (pCCA) (Legendre & Legendre 1998) to investigate how assemblage composition varied in relation to the gradients derived from the Habitat PCA. This analysis provides information on what species contribute to differences in assemblage composition between transects (i.e. β-diversity), and how such differences are driven by variation in habitat characteristics between transects (i.e. landscape heterogeneity) (Legendre, Borcard & Peres-Neto 2005; Tuomisto & Ruokolainen 2006). The pCCA was carried out separately for high- and low-intensity farmland, using the presences of the most widespread species, i.e. species with >25% of occurrences in the dataset considering the two 3-year periods. We used the habitat gradients obtained by PCA as constraining variables, and the sampling period as a conditioning variable. Model building was based on a forward-backward stepwise procedure, using Monte Carlo permutation tests with 10 000 permutations (Oksanen *et al.* 2016).

Analyses were performed in R 3.2.3 (R Core Team 2016), using 'psych' (Revelle 2015) and 'GPArotation' (Bernaards & Jennrich 2005) for PCA, 'lm' for multiple linear models, 'ecodist' (Goslee & Urban 2007) for MRM, and 'vegan' (Oksanen *et al.* 2016) for pCCA.

Results

HABITAT PATTERNS AND LANDSCAPE HETEROGENEITY

In high-intensity farmland, the Habitat PCA extracted five axes (74·9% of variation; Tables S3), three of which showed significant variation between 1995–1997 and 2010–2012 in mean transect scores (Table 1), reflecting temporal habitat changes. Over time, there were increases in permanent crops and crop patch size, and declines in irrigated crops, crop richness and edge density ($PC2_{high}$; 21·5%); increases in pastures and water bodies ($PC4_{high}$; 10·3%); and increases in annual irrigated crops and declines in open fields with scattered trees, annual dry crops and fallows ($PC5_{high}$; 9·2%). No significant temporal changes were found along the gradient from predominantly agricultural habitats, with larger crop patches, to more natural habitats with higher cover by streams and woodlands, and higher natural habitat richness and edge density ($PC1_{high}$; 23·4%), nor along the gradient reflecting increases in open woodland cover and natural habitat patch size ($PC3_{high}$; 10·5%). Regarding landscape heterogeneity, the multivariate dispersion of transect scores did not change significantly over time, but dispersion increased significantly along $PC2_{high}$ and $PC4_{high}$ (Table 1).

In low-intensity farmland, mean transect scores varied significantly across time periods in two out of six axes extracted from the Habitat PCA (82·3% of variation; Tables 1 and S4). In 2010–2012, there were increases in permanent pastures at the expense of annual dry crops and fallows ($PC3_{low}$; 11·8%), and increases in water bodies ($PC5_{low}$; 7·6%). No changes were found along the gradients reflecting increases in predominantly agricultural habitats, with larger crop patches, at the expense of natural habitats with higher cover by shrubland, streams and woodlands, more natural habitat types, and higher edge densities ($PC1_{low}$; 26·7%); increases in agricultural habitats at the expense of habitats with more open woodland and larger natural habitat patches ($PC2_{low}$; 18·1%); increases in arable land with scattered trees ($PC4_{low}$; 9·7%); and increases in annual irrigated crops ($PC6_{low}$; 8·4%). Overall landscape heterogeneity did not change significantly over time, but heterogeneity increased significantly along $PC5_{low}$ and declined along $PC6_{low}$ (Table 1).

BIRD DIVERSITY

The number of transects was always sufficient to record over 90% of species in each farmland area and period (Fig. S1). The estimated total number of species (γ-diversity) was much lower in high- than in low-intensity farmland in 1995–1997, but not in 2010–2012, when richness increased markedly in both areas (Fig. 2). A similar pattern was found for farmland and SPEC1-3 species groups, while the richness of steppe birds remained higher in low-intensity farmland in both periods, and variation between periods was much smaller (Fig. 2). Overall, variation in α-diversity was broadly similar to that of γ-diversity, albeit with a less pronounced increase between time periods, particularly in high-intensity farmland.

Variation in β_{Tot} was significantly affected by farmland area, sampling period and their interaction (Table 2). In general, β_{Tot} was much higher in low- than in high-intensity farmland in 1995–1997, but the two converged to much the same values in 2010–2012, mainly due to a sharp increase in high-intensity, and a small decline in low-intensity farmland (Fig. 3). Similar results were found

Table 1. Temporal variation between 1995–1997 (T0) and 2010–2012 (T1) in habitat patterns and landscape heterogeneity in the study area. Habitat change was estimated from paired *t*-tests comparing the mean scores of bird sampling transects along the axis extracted from principal component analysis of habitat variables (PC#), in high- and low-intensity farmland (Tables S3 and S4). Landscape heterogeneity was estimated from paired *t*-tests comparing the dispersion of scores, either along each axis (PC#) or in multivariate space (All PC). Bold denotes $P < 0{\cdot}05$

	Habitat patterns				Landscape heterogeneity			
Habitat gradient	T0	T1	*t*	*P*	T0	T1	*t*	*P*
High-intensity farmland (n = 28)								
PC1$_{\text{high}}$ (agricultural to natural habitats)	−0·12	0·12	1·98	0·058	0·87	0·72	−0·94	0·353
PC2$_{\text{high}}$ (annual irrigated to permanent crops)	**−0·38**	**0·38**	**3·75**	**0·001**	**0·42**	**0·99**	**4·06**	**<0·001**
PC3$_{\text{high}}$ (open woodlands and natural habitat patches)	0·13	−0·13	−1·32	0·197	0·60	0·63	0·13	0·894
PC4$_{\text{high}}$ (permanent pastures and water bodies)	**−0·36**	**0·36**	**2·91**	**0·007**	**0·35**	**0·81**	**2·46**	**0·018**
PC5$_{\text{high}}$ (annual irrigated crops to arable land with scattered trees)	**0·27**	**−0·27**	**−3·16**	**0·004**	0·80	0·57	−1·24	0·220
All PC$_{\text{high}}$					1·94	2·02	0·37	0·711
Low-intensity farmland (n = 43)								
PC1$_{\text{low}}$ (agricultural to natural habitats)	0·01	−0·01	−0·22	0·830	0·81	0·79	−0·17	0·864
PC2$_{\text{low}}$ (agricultural habitats to open woodlands)	−0·02	0·02	0·88	0·384	0·74	0·70	−0·23	0·818
PC3$_{\text{low}}$ (permanent pastures to annual dry crops and fallows)	**0·40**	**−0·40**	**−4·89**	**<0·001**	0·77	0·68	−0·69	0·491
PC4$_{\text{low}}$ (arable land with scattered trees)	−0·01	0·01	0·20	0·846	0·67	0·62	−0·25	0·799
PC5$_{\text{low}}$ (water bodies)	**−0·20**	**0·20**	**2·92**	**0·006**	**0·51**	**0·94**	**3·18**	**0·002**
PC6$_{\text{low}}$ (annual irrigated crops)	0·17	−0·17	−1·67	0·102	**0·79**	**0·34**	**−2·67**	**0·011**
All PC$_{\text{low}}$					2·15	2·20	0·27	0·790

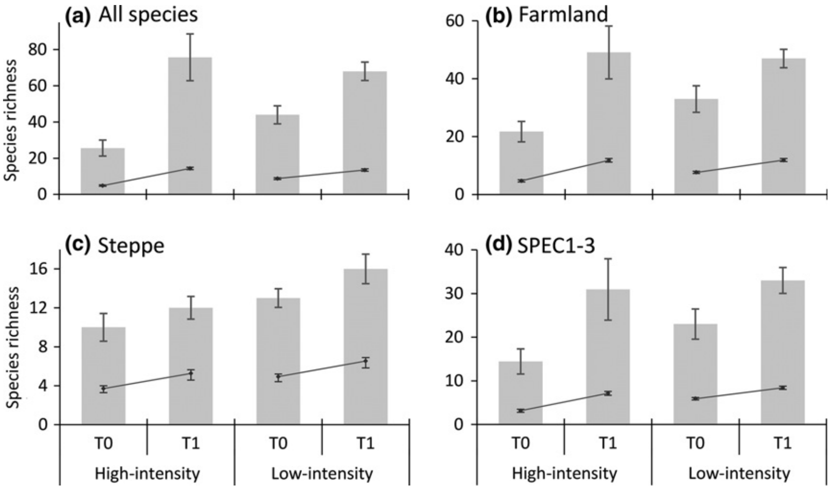


Fig. 2. Estimates of α-diversity (dots) and γ-diversity (bars) of the total (a), farmland (b), steppe (c) and species of European conservation concern (SPEC1-3; d) bird assemblages, in high- and low-intensity farmland, before (1995–1997) and after (2010–2012) the CAP reform of 2003. We estimated α-diversity as the mean (±SE) species richness per transect, and γ-diversity (±95% confidence intervals) using Chao's estimator (Fig. S1).

for β_{Repl} of total, farmland and SPEC1-3 species (Fig. 3, Table 2), with sharp increases in high-intensity farmland and stability or slight declines in low-intensity farmland (Fig. 3). This pattern was broadly similar but not statistically significant for steppe birds (Fig. 3, Table 2). There were declines between time periods for β_{RichDiff} of total, farmland and SPEC1-3 species, while β_{RichDiff} of SPEC1-3 species was higher in high- than in low-intensity farmland (Table 2; Fig. 3). There were no interaction effects for β_{RichDiff}.

EFFECTS OF LANDSCAPE HETEROGENEITY ON BETA DIVERSITY

In high-intensity farmland, there were only a few significant relations between β-diversity and landscape heterogeneity (Table S5). In 1995–1997, β_{RichDiff} and β_{Repl} of the total assemblage were positively and negatively related, respectively, to heterogeneity along PC5$_{\text{high}}$ (annual irrigated crops vs. arable land with scattered trees). In 2010–2012, β_{Repl} of the total and farmland bird assemblages were positively related to heterogeneity along PC2$_{\text{high}}$ (annual irrigated vs. permanent crops).

In low-intensity farmland, there were several significant relations between β-diversity and landscape heterogeneity (Table S6). There were often significant positive relations between β_{Tot}, β_{Repl} (mainly in 1995–1997), and β_{RichDiff} (mainly in 2010–2012) and the geographical distance between transects. In both periods, β_{Tot} and β_{Repl} were often positively related to heterogeneity along PC1$_{\text{low}}$ (more agricultural vs. more natural habitats) and PC2$_{\text{low}}$ (more agricultural habitats vs. open woodland) gradients,

Table 2. Models relating bird total beta diversity (β_{tot}), species replacement (β_{Repl}) and species richness differences ($\beta_{\mathrm{RichDiff}}$), to time period [1995–1997 (0) vs. 2010–2012 (1)] and farmland area [high-intensity (0) vs. low-intensity (1)]. For each model, we present the estimated coefficients (Coef) and standard error (SE), and their statistical significance for two-tailed tests (*P*). Significant differences ($P < 0{\cdot}05$) are in bold and negative coefficients are underlined. A positive interaction coefficient implies that diversity metrics increased more in low- than in high-intensity farmland; negative coefficients indicate the opposite trend

	Time period			Farmland area			Period × area		
Beta diversity metric	Coef	SE	*P*	Coef	SE	*P*	Coef	SE	*P*
All species									
β_{tot}	**0·09**	**0·01**	**0·001**	**0·10**	**0·01**	**<0·001**	**−0·10**	**0·01**	**0·004**
β_{Repl}	**0·22**	**0·01**	**<0·001**	**0·15**	**0·01**	**0·003**	**−0·21**	**0·02**	**0·003**
$\beta_{\mathrm{RichDiff}}$	**−0·14**	**0·01**	**0·011**	−0·05	0·01	0·287	0·12	0·02	0·085
Farmland									
β_{tot}	**0·08**	**0·01**	**0·001**	**0·10**	**0·01**	**<0·001**	**−0·10**	**0·01**	**0·002**
β_{Repl}	**0·19**	**0·01**	**<0·001**	**0·19**	**0·01**	**<0·001**	**−0·21**	**0·02**	**0·003**
$\beta_{\mathrm{RichDiff}}$	**−0·11**	**0·01**	**0·038**	-0·08	0·01	0·063	0·11	0·02	0·086
Steppe									
β_{tot}	**0·08**	**0·01**	**0·038**	**0·13**	**0·01**	**<0·001**	**−0·11**	**0·02**	**0·018**
β_{Repl}	0·08	0·02	0·164	**0·14**	**0·01**	**0·004**	−0·09	0·02	0·170
$\beta_{\mathrm{RichDiff}}$	0·00	0·02	0·931	−0·01	0·01	0·866	−0·02	0·02	0·759
SPEC 1-3									
β_{tot}	**0·09**	**0·01**	**<0·001**	**0·09**	**0·01**	**0·001**	**−0·10**	**0·01**	**0·003**
β_{Repl}	**0·24**	**0·02**	**<0·001**	**0·22**	**0·01**	**<0·001**	**−0·23**	**0·02**	**0·006**
$\beta_{\mathrm{RichDiff}}$	**−0·14**	**0·01**	**0·023**	**−0·13**	**0·01**	**0·020**	0·13	0·02	0·110

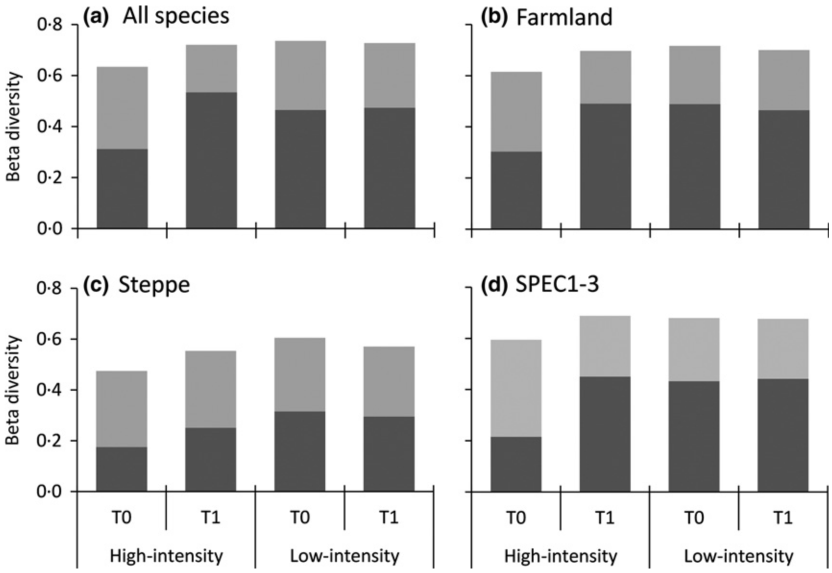
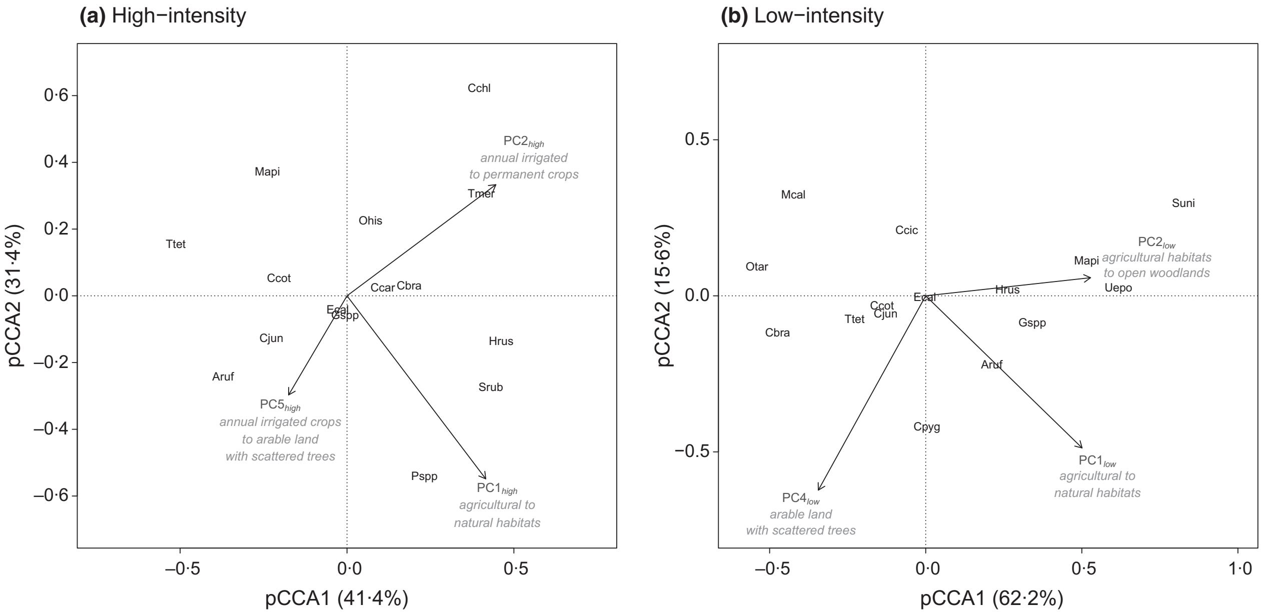


Fig. 3. Estimates of total beta diversity, and its species replacement (dark grey) and richness difference (light grey) components, for the total (a), farmland (b), steppe (c) and species of European conservation concern (SPEC1-3; d) bird assemblages, in high- and low-intensity farmland, before (1995–1997) and after (2010–2012) the CAP reform of 2003.

while relations for $\beta_{\mathrm{RichDiff}}$ tended to be negative. In 2010–2012, β_{Repl} and $\beta_{\mathrm{RichDiff}}$ of steppe birds were negatively and positively related, respectively, to heterogeneity along $\mathrm{PC4}_{\mathrm{low}}$ (increasing cover by arable land with scattered trees).

BIRD ASSEMBLAGE VARIATION IN RELATION TO LANDSCAPE HETEROGENEITY

In high-intensity farmland, the first pCCA (41·4% of variance) reflected a progressive replacement of steppe (little bustard) and some generalist farmland (quail *Coturnix coturnix*, zitting cisticola *Cisticola juncidis*, red-legged partridge *Alectoris rufa*, and bee-eater *Merops apiaster*) species, by other generalist farmland (sparrows *Passer* spp., goldfinch *Carduelis carduelis*, and barn swallow *Hirundo rustica*) and non-farmland (stonechat *Saxicola rubicola*, blackbird *Turdus merula*) species, and was significantly associated with gradients from more agricultural to more natural habitats ($\mathrm{PC1}_{\mathrm{high}}$, $F = 3{\cdot}56$, $P < 0{\cdot}001$), and of increasing cover by permanent vs. annual irrigated crops ($\mathrm{PC2}_{\mathrm{high}}$, $F = 3{\cdot}31$, $P < 0{\cdot}001$) (Fig. 4a). The second pCCA (31·4%) reflected a replacement between species associated with either increasing cover by permanent crops ($\mathrm{PC2}_{\mathrm{high}}$; bee-eater, greenfinch *Chloris chloris*, black-eared wheatear *Oenanthe hispanica*, and blackbird),


(a) High−intensity

(b) Low−intensity

Fig. 4. Biplot of the first two axes extracted from a partial canonical correspondence analysis (pCCA) in the high- (a) and low-intensity (b) farmland areas, showing the influence of landscape heterogeneity described by the main habitat gradients (arrows) on variation in bird assemblage composition (β-diversity). The proportion of total variation represented in each axis is also provided. Species abbreviations are provided in Table S1.

or with more natural habitats ($\mathrm{PC1_{high}}$) and arable land with scattered trees ($\mathrm{PC5_{high}}$, $F = 1\cdot83$, $P = 0\cdot042$), such as red-legged partridge, zitting cisticola, barn swallow, stonechat and sparrows.

In low-intensity farmland, the first pCCA (62·2%) reflected the replacement of steppe bird species of conservation concern such as great bustard, little bustard, calandra lark *Melanocorypha calandra*, and short-toed lark, by more generalist farmland species of lower concern such as bee-eater, *Galerida* larks, barn swallow, and red-legged partridge, and was significantly associated with gradients from more agricultural habitats to either more natural habitats ($\mathrm{PC1_{low}}$, $F = 5\cdot59$, $P < 0\cdot001$) or habitats with higher cover by open woodlands and large natural patches vs. agricultural habitats ($\mathrm{PC2_{low}}$, $F = 5\cdot72$, $P < 0\cdot001$) (Fig. 4b). The second pCCA (15·6%) was mainly related to increasing cover by arable land with scattered trees ($\mathrm{PC4_{low}}$, $F = 3\cdot97$, $P < 0\cdot001$) and, to a lesser extent, to the agricultural-natural gradient ($\mathrm{PC1_{low}}$), which was associated with the replacement of species such as white stork, great bustard and calandra lark, by species such as Montagu's harrier *Circus pygargus*, red-legged partridge and little bustard.

Discussion

Our study supported the idea that the expansion of previously scarce land uses after the CAP reform of 2003 contributed to increasing landscape heterogeneity, mainly due to spreading out of permanent crops (i.e. olive groves) in high-intensity farmland (Ribeiro *et al.* 2014). Also, we found that α-diversity was the main driver of the temporal increase in γ-diversity in low-intensity farmland, while both α- and β-diversity (β_{Repl}, but not $\beta_{\mathrm{RichDiff}}$) strongly contributed to increase γ-diversity in high-intensity farmland. These patterns were largely similar for all species groups, albeit much less markedly for steppe birds. There were significant relationships between β-diversity and landscape heterogeneity, but the actual land-use types influencing such relationships varied between areas, time periods and species group considered. Finally, we found that β-diversity was associated with the spatial replacement of species with contrasting habitat affinities along the main gradients of environmental heterogeneity, involving in some cases the replacement of steppe birds of high conservation concern by more common and generalist species. Overall, our study supports the value of β-diversity in conservation research (Socolar *et al.* 2016), by showing that information on patterns and drivers of spatial variation in assemblage composition add significantly to the analysis of local species richness for providing meaningful conservation management prescriptions on farmland.

Before the CAP reform (1995–1997), the higher bird diversity observed in low- than in high-intensity farmland was probably a consequence of its more favourable agricultural habitats and landscape heterogeneity patterns. During this period, the low-intensity area was dominated by a traditional farming system (Ribeiro *et al.* 2014), with high α-diversity likely supported by the presence of favourable habitats such as woodlands, riparian vegetation and fallows (Delgado & Moreira 2000; Stoate, Araújo & Borralho 2003; Santana *et al.* 2017a), and probably also by beneficial crop management practices (Ribeiro *et al.* 2016b). Likewise, our results suggest that high β-diversity was supported by high landscape heterogeneity, particularly with that associated with the gradient from natural to agricultural habitats. This gradient strongly affected spatial variation in assemblage composition, primarily through species replacement (β_{Repl}). The favourable conditions for both α- and β-diversity thus probably contributed to the relatively high γ-diversity estimated in low-intensity farmland.

In marked contrast, the low diversity observed in high-intensity farmland in 1995–1997 probably resulted from the prevalence of a farming system specialised on annual irrigated crops (Ribeiro *et al.* 2014), which was likely associated with poor bird habitats and landscape homogeneity (Ribeiro *et al.* 2016a,b). These crops tend to support low α-diversity in Mediterranean farmlands, probably due to their structural characteristics, the heavy use of agro-chemicals and other unfavourable management practices (Stoate, Araújo & Borralho 2003; Brotons, Mañosa & Estrada 2004; Santana *et al.* 2017a). The production of annual irrigated crops is also associated with low landscape heterogeneity (Ribeiro *et al.* 2016b), which probably explains the low β-diversity in high-intensity farmland, and the lack of consistent relations between β-diversity and landscape heterogeneity observed in this area. Although we found a tendency similar to that of low-intensity farmland for assemblage composition changing along the gradient from natural to agricultural habitats, this was probably not sufficient to increase the overall β-diversity due to the low representation of natural habitats in high-intensity farmland (Santana *et al.* 2017a). Whatever the mechanism, these low values of both α- and β-diversity were responsible for the low γ-diversity observed in high-intensity farmland before the CAP reform of 2003.

After the CAP reform (2010–2012), diversity metrics (except $\beta_{\mathrm{RichDiff}}$) largely increased and converged in high-intensity farmland to the values observed in low-intensity farmland. It is unlikely that these changes were primarily due to biases arising from variations in species detectability, because the open habitats with high visibility were largely retained across sampling periods in low-intensity farmland, while the number of species detected in high-intensity farmland increased markedly despite the expansion of closed habitats with potentially lower visibility (i.e. permanent crops). It is more likely that the increase in α-diversity observed in low-intensity farmland reflected a positive effect of conservation management of the SPA, without any noticeable negative effects of the transition from traditional to livestock specialised farming systems (Ribeiro *et al.* 2014; Santana *et al.* 2014). This farming system change did not affect the main gradients of landscape heterogeneity (Ribeiro *et al.* 2016b; this study), which probably explains the lack of change in β-diversity observed in this farmland area. Regarding high-intensity farmland, the increase in α-diversity was probably due to the expansion of olive groves at the expense of annual irrigated crops, providing habitat for a range of woodland and shrubland species that were previously absent or scarce in this area (Santana *et al.* 2014, 2017a). This change also contributed to increased landscape heterogeneity, which was likely responsible for the observed increase in β-diversity, mainly due to species replacement (β_{Repl}) among sites dominated by contrasting agricultural habitats. In fact, the gradient from annual irrigated crops to olive groves was strongly associated with spatial variation in assemblage composition, thereby promoting the coexistence of more species. Overall, therefore, while the increase in γ-diversity observed in low-intensity farmland was mainly driven by increasing α-diversity, both α- and β-diversity were responsible for the increase in γ-diversity in high-intensity farmland.

CONSERVATION IMPLICATIONS

This study illustrates how β-diversity can be used to provide practical insights on the management of specific farmland areas, beyond those supported solely on information from the local patterns of assemblage richness and composition (e.g. Delgado & Moreira 2000; Stoate, Araújo & Borralho 2003; Santana *et al.* 2014, 2017a). In our low-intensity farmland area, results suggest that management should be directed at maintaining a stable β-diversity, with any temporal increases in β-diversity potentially reflecting negative conservation outcomes. This is because the area is devoted to steppe bird conservation, and high β-diversity was associated with the spatial replacement of steppe bird species by species of low conservation concern. Therefore, maintaining the dominance of open agricultural habitats is critical in this and possibly other farmland areas (e.g. Báldi and Batáry 2011), even though this may be negative for landscape heterogeneity, and for overall β- and γ-diversity. In contrast, managing for high β-diversity may be sensible in our high-intensity farmland area, where increases in β-diversity after the CAP reform of 2003 probably reflect positive conservation outcomes. This is because increasing overall diversity rather than the diversity of any particular species group is generally the main goal in high-intensity farmland (e.g. Fahrig *et al.* 2011; Karp *et al.* 2012), and in our case this was favoured by recent increases in landscape heterogeneity associated with the expansion of olive groves. Therefore, maintaining a patchwork of arable and permanent crops may be a key management goal in this area, as this provides conditions for both farmland and woodland and shrubland species at the landscape scale (Santana *et al.* 2017a), and thus high β- and γ-diversity. Further expansion of olive groves may turn out to be negative, however, if it leads to progressive homogenisation of the landscape, requiring this potential outcome to be assessed through continued monitoring of β-diversity.

In general, our study underlined the value of β-diversity to inform agricultural policies and conservation actions on farmland, supporting previous suggestions that it may be essential to capture processes that are hard or impossible to detect using only local diversity metrics

(Clough *et al.* 2007; Gaston *et al.* 2007; Monnet *et al.* 2014; Socolar *et al.* 2016; Żmihorski *et al.* 2016). First, our results illustrated the importance of β-diversity to understand the consequences of land-use changes, as focusing solely on α-diversity would have missed important links between biodiversity and anthropogenic drivers. This was particularly evident in high-intensity farmland, where variation in γ-diversity was mainly driven by β-diversity. Second, the analysis of β-diversity helped identify the main land-use types shaping functional landscape heterogeneity (sensu Fahrig *et al.* 2011), which is critical for farmland conservation management. In fact, although there was a variety of land uses shaping a range of habitat gradients, only heterogeneity associated with the gradients from agricultural to natural habitats in the low-intensity farmland area, and from arable to permanent crops in the high-intensity farmland area, could be considered functional, in the sense that they strongly affected spatial variation in assemblage composition. Finally, our results showed that while temporal variations in β-diversity may be used to assess biodiversity trends, the meaning of such changes should be carefully considered, as we found high levels of β-diversity to be linked with potentially negative conservation outcomes in low-intensity farmland. This supports the view that higher β-diversity does not necessarily equate to higher conservation value (Socolar *et al.* 2016), and thus that the management of landscape heterogeneity and β-diversity should be fine-tuned in relation to well-defined conservation goals (e.g. Báldi & Batáry 2011).

Authors' contributions

J.S. and P.B. conceived the study; J.S. produced land cover maps with help of L.R., P.B., P.F.R. and F.M.; J.S. analysed the data with the assistance of M.P., P.B. and J.T.R.; J.S. wrote the first draft of the manuscript with the assistance of P.B. and J.T.R.; L.R. collected part of bird data and prepared bird data database with help of J.S.; all authors read and commented on drafts of the manuscript.

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Data accessibility

Bird and habitat data used in this study are available through the Dryad Digital Repository https://doi.org/10.5061/dryad.kp3fv (Santana *et al.* 2017b).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig S1 Sample-size-based rarefaction (solid lines) and extrapolation (dotted lines) curves (a–d), and sample completeness curves (e–h) in each farmland area and sampling period using Chao's estimator and q = 0 (species richness).

Table S1 List of bird species recorded in high- and low-intensity farmland areas in southern Portugal, before (1995–1997) and after (2010–2012) the CAP reform of 2003.

Table S2 Formulation of the indices used to estimate beta diversity and its components following Podani & Schmera (2011), Carvalho, Cardoso & Gomes (2012) and Carvalho *et al.* (2013).

Table S3 Loadings of habitat variables in high-intensity farmland on varimax rotated axes ($PC\#_{high}$) extracted from a principal component analysis (PCA).

Table S4 Loadings of habitat variables in low-intensity farmland on varimax rotated axes ($PC\#_{low}$) extracted from a principal component analysis (PCA).

Table S5 Summary of models relating β-diversity metrics (total beta diversity, β_{Tot}; species replacement, β_{Repl}; species richness difference, $\beta_{RichDiff}$) to variation in landscape heterogeneity in high-intensity farmland.

Table S6 Summary of models relating β-diversity metric (total beta diversity, β_{Tot}; species replacement, β_{Repl}; species richness differences, $\beta_{RichDiff}$) to variation in landscape heterogeneity in low-intensity farmland.