Birds in a complex agricultural landscape in Central Greece: the role of landscape elements and the landscape matrix

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Agricultural environments play a key role in the conservation of biodiversity in Europe. The vast majority of agricultural lands, however, are located in the non-designated wider countryside embedding protected Natura 2000 sites with little or no protection of habitats. The European Union wants to halt and reverse biodiversity loss within the next decade by focusing on sustainable agriculture as one out of six main drivers of biodiversity loss. Indeed, many farmland bird species have shown pronounced population declines over the last 50 years with ever-increasing habitat modification due to changing farming systems. This process of rapid habitat modification may have stabilized in Western Europe, but it is very likely to continue in Central and Southern Europe. The effects of landscape composition and configuration on bird assemblages have been scarcely studied in the Balkan Peninsula, despite its important contribution to the subcontinent's biodiversity. We assessed breeding bird assemblages-environment relationships by incorporating environmental predictors at two spatial scales. Birds were surveyed in 90 plots by stratified sampling in eight *a priori* defined landscape types. The objective of this study was to assess the bird composition in the eight landscape types as well as to quantify the independent and confounding influences of local patch level predictors and broader landscape-level predictors using variation partitioning by running multiple CCA analyses. Samples with dense vegetation structures and samples with lesser amounts of vegetation among the eight landscape types appeared to hold significant different species compositions as it is shown by analysis of similarity. These findings were also reflected by the CCA analysis and the environmental predictors were able to distinguish bird communities adequately well. Almost one third (29.6%) of the total variation in species abundance data was explained by both sets of predictor variables together. Confounding influences of the environmental predictors explained 6.5% of the variation, which indicates that there is a remarkable interdependence of the focal scales. This might have major implications for bird conservation planning and land management in the agricultural countryside outside and within protected Natura 2000 sites.

Key words: Breeding bird assemblage, Mediterranean, variation partitioning, wider countryside, conservation.

INTRODUCTION

Agricultural land accounts for almost half of the total EU-27 land area, providing crucial habitats for a wide range of the total wildlife resource (Bunce *et al.*, 2008; Stoate *et al.*, 2009). It has been estimated that 50% of all species in Europe depend on agricultural

habitats (EC, 2008) and these habitats support a high proportion of the population of many threatened bird species as well as declining populations of common bird species (Tucker & Heath, 1994; Birdlife International, 2004; PECBMS, 2007). Therefore, agricultural environments play a key role in the conservation of biodiversity in Europe.

Post-war agricultural policies in the EU (e.g. the Common Agricultural Policy – CAP) resulted in an unprecedented increase in agricultural productivity,

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with a shift from extensively-managed farmed land, such as pastures, fallow meadows and field margins to intensive, large-scale, high-input and heavily mechanised farmed land (Reidsma *et al.*, 2006; Stoate *et al.*, 2009). The majority of the severe declines in populations of farmland birds (and other wildlife) across Europe have been associated with either the progressive intensification of agricultural practices (Donald *et al.*, 2001; Newton, 2004; Donald *et al.*, 2006; Butler *et al.*, 2007) and the attrition of natural and semi-natural habitats (Donald *et al.*, 2006; Reidsma *et al.*, 2006) or the concurrent land abandonment in more isolated or less productive regions (Preiss *et al.*, 1997; Tucker & Evans, 1997; Wretenberg *et al.*, 2006). In the study of Kallimanis *et al.* (2008), the authors found that agriculture within Greek protected Natura 2000 sites did not have a negative effect on landscape habitat diversity. However, most agricultural lands in Greece (58%) are not irrigated and thus not intensively cultivated, which distinguishes them from large habitat modifications in Western Europe.

The process of rapid habitat modification in Western Europe may have been stabilized, but it is very likely to continue in Central and Southern Europe (Bunce *et al.*, 2008). Moreover, causes of farmland bird population changes may differ across Europe, leading to a need for further research into the effect of farmland management in different parts of the continent (Reif *et al.*, 2008). Mediterranean agricultural landscapes are very characteristically mosaics of different land-uses (Blondel *et al.*, 2010). Anthropogenic activities such as agriculture, livestock grazing, irrigation, cutting and burning have influenced the Mediterranean area for millennia, much longer than elsewhere in Europe, and a complex co-evolution between man and the ecosystem is its main characteristic (Grove & Rackham, 2003), with intensification and abandonment of agricultural activities and methods further influencing the outcome of this co-evolution.

The Birds Directive (2009/147/EC), EU's oldest nature legislation for the protection of all wild bird species naturally occurring in the Union, already designates 14% of total EU land surface as Special Protection Areas (SPAs) which may include significant amounts of agricultural lands. Nevertheless, the vast majority of agricultural lands are located outside the boundaries of these protected sites with little or no protection of habitats (Bunce *et al.*, 2008). According to the EU, the Natura 2000 network alone will not be able to conserve biodiversity in Europe without action also being taken in the wider countryside (EC, 2008). In this sense, EU has focused on the establishment and integration of biodiversity concerns into other policy areas such as agriculture and regional development (EC, 2010). On May 3rd, 2011 the EU Commission published a new landmark strategy designed to halt and reverse biodiversity loss within the next decade. It states six ambitious targets that focus on the main drivers of biodiversity loss and focuses on actions and measures to realize these targets. One target is to ensure the sustainability of agriculture and forestry by ensuring the conservation of biodiversity and providing measurable improvements in the conservation status of species and habitats that depend on or are affected by agriculture (EC, 2011).

Sustainable agriculture should incorporate the increasing awareness about the importance of local countryside elements, such as plantations, scattered trees, hedges and pasture lands for biodiversity (Daily *et al.*, 2001; Manning *et al.*, 2009), as well as processes at the landscape scale. It is suggested that landscape composition (amount of certain patch types present) is generally more important than landscape configuration (spatial distribution of patches in a landscape), with the latter becoming increasingly important only at low levels of habitat area (Fahrig, 2001, 2002; Cushman & McGarigal, 2004).

We focus on breeding passerine birds in a Mediterranean mosaic agricultural landscape in Central Greece and quantify the similarity of bird species composition among eight predefined landscape types. We also assess the relative importance of environmental predictors at two spatial scales: at local patch-level and broader landscape-level scale. The effects of landscape composition and configuration on bird assemblages have been scarcely studied in the Balkan (part of the Mediterranean Basin), despite its important contribution to the subcontinent's biodiversity (Blondel *et al.*, 2010). By applying variation partitioning, we assessed which of the environmental predictors define breeding bird assemblages and we determined the independent and confounding effects of these patch- and landscape-level predictors. This multiple scale partitioning approach is efficient to reveal assemblage-environment relationships, since individual organisms experience and respond to environmental heterogeneity across a range of scales (Levin, 1992).

MATERIALS AND METHODS

Study area

The study area is situated in Central Greece in the periphery of Thessaly, approximately 21 km north of the city of Elassona. It covers 4200 ha (7 km × 6 km) (Fig. 1). The study area includes the small village of Dolichi (*ca* 40°03′39″N, 22°09′53″E) situated east of Mount Olympos (2917 m) and the altitude of the study area ranged from 500 m to 800 m. The climate is sub-Mediterranean, which is at the transition between a Mediterranean and a continental climate (Grove & Rackham, 2003).

The study area is situated in the *Ostryo-Carpinion* vegetation zone, characterised by meso- and supra-Mediterranean sclerophyllous and deciduous forests with few coniferous species (mixed forests) (Spanos *et al.*, 2003). Spontaneous vegetation is mainly comprised of prickly oak (*Quercus coccifera*), the dominant species due to its high grazing and fire resistance, its growth capacity and its phenotypic plasticity (Spanos *et al.*, 2003).

The undulating northern part of the study area is dominated by intensively grazed pastures while steeper hills are covered with degraded maquis-like vegetation (with *Q. coccifera* thickets). The plains to the south are covered by intensively managed cropland and grazing pastures. Livestock is herded in unfenced collective grazing grounds ('commons'). These common grazing pastures have a savannah-like appearance with dispersed trees and shrubs, mainly *Pyrus amygdaliformis* and *Quercus coccifera* (see Fig. 1 and see online supplementary material, Fig. S1F).

Sampling design

1. Environmental predictors

An identification and classification of the landscape types were performed based on the interpretation of a pan-sharpened multi-spectral Quickbird Satellite Image of 2003 with a spatial resolution of 0.6 m. Field surveys were done during the months of November 2004 and April 2005. The visual classification of the landscape types was based on the presence and spatial distribution of the dominant vegetation together with landscape elements and land use. We defined 8 major landscape types (see online supplementary material, Fig. S1): 1. Croplands, 2. Badlands, 3. Thickets, 4. Hedgerows 5. Grasslands with scattered *Quercus coccifera* and *Pyrus amygdaliformis*, 6. Plantations, 7. Rivulet accompanying vegetation and 8. Dehesas. We apply the term 'dehesa' in Greece for a sylvo-pastoral system that can be recognized physiognomically as unfenced grasslands with an irregular orchard-like appearance of high stem evergreen trees. This description only slightly differs from the more common def-
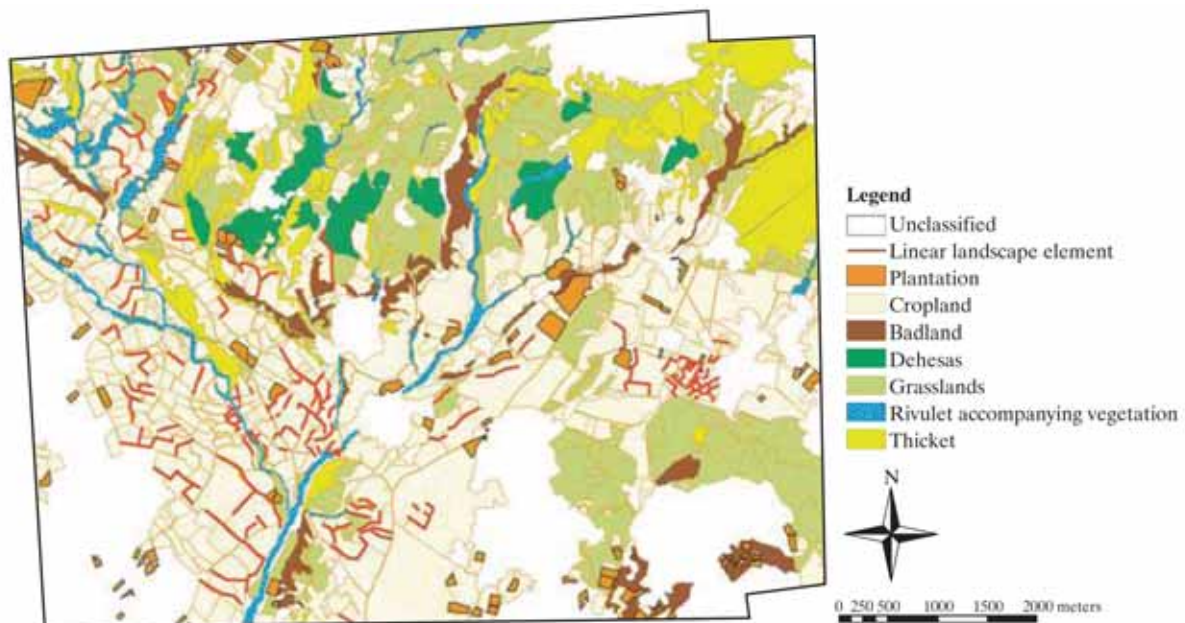

FIG. 1. Classification of the Quickbird satellite image of 2003 of the study area Livadi-Dolichi according to the eight *a priori* chosen landscape types. 'Linear landscape elements' include small and large hedgerows and other linear vegetation. The unclassified class includes clouds, cloud shadows and the village of Dolichi.

inition of dehesas according to Blondel *et al.* (1999): 'an agro-sylvo-pastoral system wherein the three main rural activities of wood-gathering, livestock husbandry, and agriculture are pursued conjointly in a single space'.

We drew 90 census points by random stratified sampling of the 8 landscape types on the Quickbird Satellite Image. At each census point we recorded patch-level environmental predictors within a 50 m radius (0.85 ha) around the observer (see online supplementary material, Table S1). As advocated by Bunce *et al.* (2008) we adopted a physiognomical approach to vegetation, however we referred to characteristic indicator species wherever necessary. Patch-level predictors were assessed by an abundance scale of 0 to 5 (with 1 being an amount or coverage interval from 0 to 20% and 5 from 80 to 100%), respectively by presence/absence (see online supplementary material, Table S1). The qualitative predictor Grazing pressure was assessed by a scale of 0 to 5, with 1 having few signs of grazing (no 'sculpted' bushes, no trampling, higher plantcoverage, etc.) and 5 indicating heavy grazing (trampled vegetation, prickly and unpalatable annuals, no or severely 'sculpted' bushes, bare soil and low plant coverage).

Based on our landscape classification with 8 landscape types, five landscape-level predictors (see online supplementary material, Table S1) were calculated for a 500 m circular buffer zone (78.5 ha) around each plot using Fragstats version 3.3 (McGarigal *et al*., 2002). The mean area of a patch (AREA_MN) is a very important piece of information because it has an intuitive and ecologically useful interpretation: bird species occurrence/abundance is often correlated with patch size (McGarigal & McComb, 1995). Edge density (ED) is an interesting metric since the total amount of edge in a landscape is directly related to the degree of spatial heterogeneity in that landscape (McGarigal & McComb, 1995). Mean perimeter-area ratio (PARA_MN) is a simple measure of shape complexity, but without standardization to a simple Euclidean shape (McGarigal & McComb, 1995). Mean edge contrast (ECON_MN) was chosen as a metric since not all edges between different patches should be treated equal. We took our knowledge and theoretical understanding of bird habitat use, based on the physiognomy of the vegetation, to assign different edge contrasts between certain different patches. We considered a strong contrast among open (cropland) and well vegetated landscape types (e.g. thicket, dehesa, etc.) and a less strong contrast

among 'hedges' and 'grassland' again with well vegetated landscape types. Edges among well vegetated landscape types were considered to be similar and no edge contrast was assigned. The Simpson's diversity index (SIDI) is a measure of landscape heterogeneity: the higher the value of this index, the higher the landscape diversity, meaning the number of different patch types increases and the proportional distribution of area among patch types becomes more equitable (McGarigal & McComb, 1995).

2. Bird census

Bird surveys were conducted during the start of the breeding season (from 03/05/2005 to 27/05/2005) by means of a 50 m fixed-radius counting method (Hutto *et al*., 1986). The observation period started at sunrise until 10:30 am and from 6:00 pm until 9:00 pm. Two counts for every plot were carried out: one in the morning and one in the evening. A first count in a plot took place in the first two weeks of May, while a second visit was planned in the last two weeks of May. With this approach we aimed to have the two visits spread as much as possible in 'time' and 'day' to include all possible variability.

The bird counts lasted approximately 15 min proceeded by an adaptation period of 5 min. The same observer performed the bird counts in order to avoid an observer effect. Twenty-six passerine bird species were considered for further statistical analysis (see online supplementary material, Table S2). All raptors species of the corvid family and aerial insectivores (e.g. bee-eater, swallows and swifts) were excluded from the analysis (their action radius does not associate with particular landscape features).

As spatial autocorrelation in the bird dataset was likely to occur at the scale of the study plots, we investigated spatial autocorrelation for bird presence-absence by using Moran's I correlograms, calculated with SAM v4.0 (Rangel *et al*., 2006).

3. Data analysis

Similarities in species composition amongst the eight landscape types were compared using one-way analysis of similarity (ANOSIM) by using PRIMER v6 (Clarke & Gorley, 2006). We used Bray-Curtis similarity indices calculated on bird species abundances to determine compositional similarities amongst the landscape types. The abundance data were square root transformed in order to downweight the contri-

butions of quantitatively dominant species to the similarities calculated between the landscape types. For each pair of landscape types a pairwise R statistic was calculated, varying between 0 (no difference) and 1 (all dissimilarities between landscape types are larger than dissimilarities among samples within either landscape type). Statistical significance of R is calculated at a 0.1% significance level through 999 permutations.

We assessed bird assemblages in relation to the environmental predictors using canonical multivariate analysis with the software program CANOCO version 4.5 (ter Braak & Šmilauer, 2002). Through a Detrended Correspondence Analysis (DCA) we determined that the avifaunal data exhibit a unimodal response distribution. Therefore, we analyzed the data using Canonical Correspondence Analysis (CCA) with biplot scaling and a focus on interspecies distances to explicitly analyse the relationship between community composition and environmental variables. CCA maximizes the dispersion of species scores following a selection of linear combinations of environmental predictors and emphasizes patterns in relative abundances. This technique is particularly useful for species data with many zero abundances (ter Braak & Šmilauer, 2002).

CCA analysis involved a forward selection procedure to obtain the smallest set of predictor variables explaining statistically significant variance in the community data. This is a standard procedure in CANOCO version 4.5 that selects at each step the predictor variables that contribute most to the explained variance in the response variables. Species abundance data were log transformed $[(\log(x+1)]$ before the CCA analysis to prevent extreme values (outliers) from unduly influencing the ordination (ter Braak & Šmilauer, 2002). We used Monte Carlo permutation (999 unrestricted permutations) to test whether there was any significant relation between bird assembly and the landscape features.

We applied variation partitioning to determine the independent and joint effects of the patch- and landscape-level predictors on bird species composition through a series of CCA analysis. We partitioned the variation into four different components: (1) the variation uniquely described by the patch-level predictors (P|L), (2) the variation exclusively explained by the landscape-level predictors (L|P), (3) the variation described by the intersection of both sets of environmental predictors (P∩L) and (4) the unexplained variation ((TI)-(P∪L)). We obtained the first component from a partial CCA where the patch-level predictors were considered as variables while the landscape-level predictors (P|L) are used as covariables, and *vice versa* for the second component (L|P). For calculating the variation explained by the intersection of both sets of environmental variables (P∩L), we carried out a CCA where patch-level predictors as well as landscape-level predictors were considered as environmental variables (P∪L) (Cushman & McGarigal, 2002; Lepš & Šmilauer, 2003).

RESULTS

Species composition similarity

The permutation distribution of the ANOSIM test statistic R was never greater or equal to the Global R (true value of R: 0.355), therefore we could reject the null hypothesis at a significance level of 0.1% that there were no differences in species composition among samples of the different landscape types. Small R values (R < 0.3) of the pairwise comparisons of the landscape types 'thicket' with 'dehesa', 'grassland', 'badland' and 'rivulet' indicate that their respective species compositions differ slightly. The same strong overlap in species composition is also true for the pairs 'hedgerows' with 'plantation', 'grassland', 'cropland' and the pairs 'grassland-plantation' and 'rivulet-badland' (Table 1). The species composition varied significantly (R > 0.6) amongst the pairwise comparisons of 'cropland' with 'dehesa', 'badland', 'rivulet', 'thicket', and 'hedgerow' with 'dehesa' and 'badland'.

Bird assemblages and environmental variables

Manual forward selection of all patch and landscape explanatory variables in CCA resulted in a reduced set of seven patch-level and three landscape-level predictors variables (Fig. 2) that significantly explained the bird-environment relation. The first axis of this full environmental model explained 11.5% of the species variance. This axis represented a gradient from high diversity landscapes (SIDI) with closed or dense vegetation structures (veg_pat) and kermes oak-cover (*Q. coccifera* bush (Qcbshcov) and high stem (Qchstcov)), to low diversity landscapes with large patches (AREA_MN) of agricultural fields (cropc), whether or not bordered by small hedgerows.

The second axis explained only 5.4% of the species data. It indicates a gradient with abundant deciduous vegetation cover (v_dc) to patches with high edge contrast (ECON_MN) and unfenced collective

TABLE 1. Analysis of similarity (ANOSIM) resemblance matrix of the 8 landscape types by using Bray-Curtis similarity indices calculated from transformed bird species abundances. The higher the value of R the greater the difference in species composition of the two landscape types compared

	Plantation	Dehesa	Grassland	Badland	Rivulet	Thicket	Cropland	Hedgerows
Plantation	—							
Dehesa	0.528*	—						
Grassland	0.232*	0.443*	—					
Badland	0.579**	0.482*	0.312**	—				
Rivulet	0.439**	0.421*	0.306**	0.120*	—			
Thicket	0.390**	0.285*	0.276**	–0.005	0.156**	—		
Cropland	0.340*	0.846**	0.333*	0.746**	0.708**	0.597**	–	
Hedgerows	0.042	0.680*	0.103	0.622**	0.484**	0.453**	0.158	—

Significance level * at 0.05 and ** at 0.01

grazing grounds with high anthropogenic disturbances (hos).

Bird species that highly correlated with kermes oak-cover (*Q. coccifera*) and Simpson's diversity index (SIDI) are the Blackbird (*Turdus merula* – Tmer), the Jay (*Garrulus glandarius* – Ggla), the Subalpine Warbler (*Sylvia cantillans* – Scan), the Chaffinch (*Frigilla coelebs* – Fcoe) and the Cirl Bunting (*Emberiza cirlus* – Ecir). The Calandra Lark (*Melanocorypha calandra* – McaK), the Common Quail (*Coturnix coturnix* – Ccot) and the Crested Lark (*Galerida cristata* – Ccri)

strongly correlate with crop cover (cropc) and mean patch area (AREA_MN). The Wheatear (*Oenanthe oenanthe* – Ooen) strongly correlated with heaps of stones (hos), as did the Syrian Woodpecker (*Dendrocopos syriacus* – Dsyr), the Red-backed Shrike (*Lanius collurio* – Lcol), the Woodchat Shrike (*Lanius senator* – Lsen), Greenfinch (*Carduelis chloris* – Cchl) and the Lesser Grey Shrike (*Lanius minor* – Lmin).

Many bird species were positioned near the intersection of the ordination axes and have a less pronounced correlation with any particular environmen-
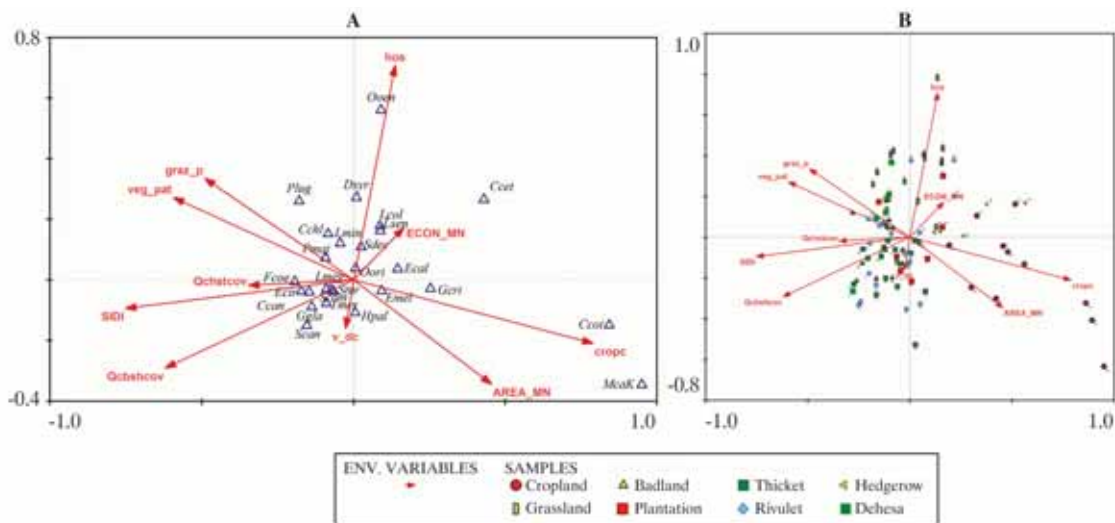

FIG. 2. Canonical correspondence analysis ordination diagram of avifauna (A) and landscape types (B) in a complex agricultural landscape in Central Greece, depicting the first two canonical axes. Axis 1 runs horizontally; axis 2 runs vertically. Environmental variables (patch- and landscape-level predictors) are represented by arrows, which point toward increasing values of that variable. A smaller angle between the ordination axis and the arrow implies greater influence of the variable on the environmental gradient of the axis. The proximity of (A) Bird species, represented by triangles and (B) samples, with indication of the assigned landscape type, indicates occurrence in similar environmental conditions.

tal predictor (e.g. the Whitethroat (*Sylvia communis* – Scom), the Golden Oriole (*Oriolus oriolus* – Oori), the Collared Dove (*Streptopelia decaocto* – Sdec), the Turtle Dove (*Streptopelia turtur* – Stur) and the Nightingale (*Luscinia megarhynchos* – Lmeg). The Eastern olivaceous warbler (*Hippolais pallidus* – Apal) was well associated with the amount of deciduous vegetation.

Variation partitioning of environmental variables

The total variation in species abundance data (total sum of the canonical eigenvalues) carried out on both sets of predictor variables was 0.815 (P∪L) or 29.6%. The unexplained variation ((TI)-(P∪L)) equalled 1.936 or 70.4%. The variation uniquely described by the patch-level predictors (P|L) was 0.476 or 17.3%, whereas the variation solely described by the landscape-level predictors (L|P) was 0.159 or 5.8%. The variation explained by the intersection of both sets of environmental predictors (P∩L) equalled 0.18 or 6.5%.

Spatial autocorrelation

Moran's I correlograms indicated only statistically significant positive autocorrelation for small-distance classes (< 500 m) for bird species presence/absence, as well as for landscape level predictors.

DISCUSSION

Species composition similarity

The eight landscape types in the study area show patterns of significantly different species composition as is shown by the analysis of similarity (Table 1). Small R values (R < 0.3) of the pairwise comparisons of bird assemblages within the landscape types 'Thicket', 'Dehesa', 'Grassland', 'Badland' and 'Rivulet' indicate that their species compositions have a large overlap with minor differences. The greatest difference (R > 0.6) in species composition was observed amongst the open landscape types with sparse vegetation and landscape types with ample vegetation (e.g. 'Cropland' and 'Hedgerows' *versus* 'Dehesa' and 'Badland'). The 'Grassland' landscape type always showed low R values, indicating that its species composition has similarities with species assemblages of all other landscape types. Since we based the classification of the landscape types on the presence and spatial distribution of the dominant vegetation together with landscape elements and land use, it might not be sur-

prising to see these differences also reflected in the species composition of the different landscape types.

These findings also show up in the ordination diagram (biplot) of samples (Fig. 2B): samples assigned to 'Cropland', 'Hedgerow' or 'Grassland' are clustered without much intermixing of samples from other landscape types, while 'Thicket','Rivulet','Dehesa' and 'Badland' appeared as one mixed cluster indicating that these landscape types were determined by similar environmental predictors.

Spatial autocorrelation

The small extent of the total landscape area and the presence of unclassified sections, did not allow for full spacing out of plots. However, the number of spatially clustered plots (e.g. 14 pairs of plots lie at a distance less than 200 m) was kept to a minimum. At a distance interval smaller than 500 m, we observed a significant spatial autocorrelation (Moran's I) for some bird presence/absence data.

We also observed a significant spatial autocorrelation (Moran's I) for the landscape level predictors at short distance intervals (< 500 m). This is due to the inevitable large overlap of the buffer zones with a diameter of 1 km in an area of about 7 km × 6 km. The 500 m radius zones are not compared or analysed *per se*, but used as the matrix for the input of environmental predictors of bird assemblages in the 50 m radius core. The above spatial autocorrelation is therefore part of the analysis of bird species composition in a complex landscape.

Bird assemblages and environmental variables

Even at the small scale of the study area and with the close proximity of respective landscape types avifauna is spatially differentiated and bird assemblages could be explained by the semi-quantitative set of patch- and landscape level predictors. By using two scales of environmental variables (patch- and landscape level) and isolating effects of each scale and both scales together, we provide a better characterization of the community-environment relationships than usually found in most researches on avian communities conducted at a single scale. Most variation partitioning studies on birds focus on forest landscapes and the relative importance of explanatory variables for bird composition (Drapeau *et al*., 2000; Cushman & McGarigal, 2002, 2004). There are only few studies on birds in a Mediterranean environment using a variation partitioning approach (e.g. Coreau

& Martin, 2007; Godinho & Rabaca, 2011) and to our knowledge, no such studies were conducted in a mosaic Mediterranean agricultural landscape.

Our study revealed that the total variation in species abundance data that could be explained by both sets of predictor variables together (P∪L) was 29.6%. The unexplained variation ((TI)-(P∪L)) was high (70.4%), however such high values are not uncommon in similar studies (Grand & Cushman, 2003; Titeux *et al.,* 2004). The variation uniquely described by the patch-level predictors (P|L) and landscape-level predictors (L|P) was 17.3% and 5.8%, respectively. These results suggest that vegetation composition and general habitat types at a local scale (patch-level predictors) seem to be more important in explaining bird distributions in our study area than broad scale landscape-level predictors. This was also found in the study by McGarigal & McComb (1995), where the non-Mediterranean landscape structure was shown not to be a dominant explanatory factor, given the large amount of unexplained variation. On the other hand, Atauri & de Lucio (2001) concluded that individual land cover types were less important than landscape heterogeneity for the avian patterns in Mediterranean landscapes. Although landscape heterogeneity can correlate with bird species richness or abundance, this species-environment relation depends probably more on the area and distribution of particular habitats within the landscape. The identity and area of key habitats and the mosaic they constitute can be more important than habitat heterogeneity in itself (Cushman & McGarigal, 2002; Heikkinen *et al*., 2004).

Nevertheless, landscape composition and landscape configuration were able to distinguish bird communities very well. The two landscape-level predictors that quantify landscape composition, Simpson's diversity index (SIDI) and mean area of a patch (AREA_MN) clearly were able to segregate bird assemblages that preferred more heterogeneous landscapes with a mosaic of many different landscape types, and assemblages that were associated with large patch sizes of a single landscape type. Bird species of the latter assemblages are the Calandra Lark (McaK), Common Quail (Ccot) and Crested Lark (Ccri). They typically prefer homogeneous, open landscapes with few and widely scattered trees or scrubs. Bird species as Blackbird (Tmer), Jay (Ggla), Subalpine Warbler (Scan), Chaffinch (Fcoe) and Cirl Bunting (Ecir) occur in more heterogeneous landscape with well vegetated landscape types.

The only significant landscape-level predictor in our analysis that quantifies landscape configuration, mean edge contrast (ECON_MN), correlated mainly with species such as Cetti's warbler (Ccet), Collared Dove (Sdec), the Red-backed Shrike (Lcol), the Woodchat Shrike (Lsen) and Corn Bunting (Mcal). Since we specified the largest edge contrast magnitude among 'cropland' and landscape types with ample vegetation, we expected a better correlation of mean edge contrast with bird assemblages of open landscapes (cropland). However, since 'cropland' clearly occurs in much larger patches than other landscape types, the mean area of a patch have a dominant influence over mean edge in determining cropland bird assemblages.

Patch-level predictors that significantly explain the bird assemblage-environment relationship were mainly based on the dominant vegetation cover in a plot. The first canonical axis of the CCA revealed a gradient of structural complexity and vegetation height ranging from open land cover types and hedgerows to increasingly closed evergreen and wooded vegetation covers. The second canonical axis describes a gradient of patches with denser deciduous vegetation (v_dc) to patches with dispersed deciduous vegetation such as unfenced collective grazing grounds with high anthropogenic disturbances (livestock grazing) (hos). The Eastern Olivaceous Warbler (Apal) is a species that was always observed in deciduous vegetation along rivers or in denser *Pyrus amygdaliformis* bushes of grassland landscape, while the Wheatear (Ooen) strongly correlates with heaps of stones (hos), and requires ample bare areas like grasslands (BWPi 2.0).

The confounding variation between both sets of environmental predictors (P∩L) equalled 6.5% which is relatively low compared to other studies (Grand & Cushman, 2003; Coreau & Martin, 2007) but explains more than the 5.8% of variation of landscape-level predictors alone (L|P). This confounding indicates that there is a remarkable interdependence of the two focal scales at patch- and landscape level.

Our results should be interpreted within limitations of this study. We based the landscape extent (78.5 ha as largest area of investigation around each plot) on the assumed maximum home range of many passerine birds. This extent might not be equally biologically relevant to all species in the analysis. The choice of the landscape extent has of course implications on the choice and meaningfulness of the landscape-level predictors included in this study. We tried

to avoid the choice of redundant predictors, however we may have failed to include other important 'metrics' to better describe the dimensions of the landscape structure. The right choice of metrics to include in the analysis is always a major issue (Cushman *et al*., 2008). Our human-perceived landscape type classifications and associated patch boundaries may be considered to be artificial and may not have captured biologically relevant boundaries for each species. Yet, our study is based on explaining assemblage-environment relationships at two scales by using a bird census during one breeding season. If bird communities vary greatly over time, then researchers are faced with less reliable data and it is advised to use bird data from two or more years (Heikkinen *et al*., 2004). However, we conjecture the local avifaunal composition in our study area to show little dynamics (turnover) over a three year period since we have performed exploratory field surveys in 2003 and 2004 and assessed no major changes in spring breeding bird composition (results not shown).

Considerations for bird conservation

Almost one third of the total variation in species abundance data was explained by both sets of predictor variables together. The confounding influences of the environmental predictors at patch- and landscape scale, indicates that there is a remarkable interdependence of the two focal scales at both patch and landscape levels. This might have major implications for conservation planning and land management in the agricultural countryside outside and within protected Natura 2000 sites. The new Biodiversity Strategy of EU for sustainable agriculture (EC, 2011) and the recent initiatives in the EU policy regarding the strengthening of a 'Green infrastructure' (i.e. the non-designated wider countryside interconnecting Natura 2000 sites) (EC, 2010), should focus on relevant (interdependent) scales of management to keep target species in a favourable conservation status. Both local functional habitat patches and small-scale landscape elements in a context of the composition and heterogeneity of the whole agricultural matrix should be taken into account if the EU wants to halt, and reverse, biodiversity loss within the next decade (2010-2020).

Most species we observed would now still be considered common (BirdLife International, 2004), and therefore of least concern. While nature conservation is understandably focused on rare and uncommon species, concern is growing regarding 'common species' because of their drastic recent declines in abundance and because of their proportionately greater role in the ecosystem. They are the main victims of habitat loss, fragmentation, and degradation (Gaston, 2010) and common bird species are accepted as bioindicators of ecosystem health in the absence of standard measures of biodiversity (Gregory *et al*., 2005).

Current insights about restoring farmland bird populations share a common assumption: if agricultural practice has reduced populations hitherto, then agricultural practice can restore the losses (Ormerod & Watkinson, 2000). Therefore, a major challenge for landscape management will be to identify practices that prevent long-term habitat loss for birds while incorporating the short- and long-term needs of local people, in the study area as related to sheep and goat herding and agricultural modernization.

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