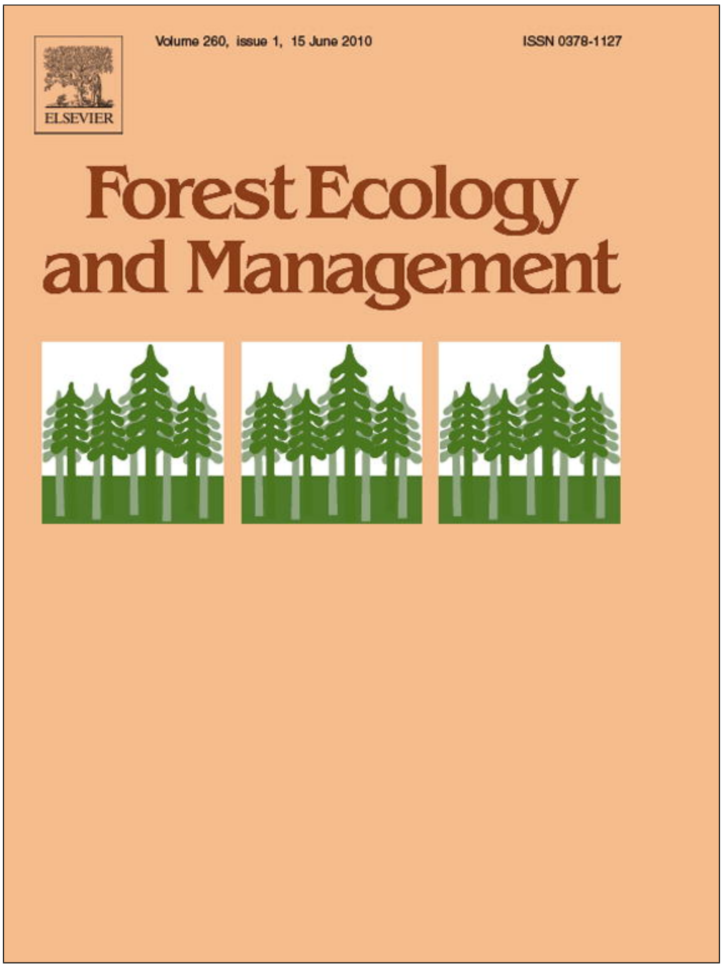
Volume 260, issue 1, 15 June 2010
ISSN 0378-1127
ELSEVIER
Forest Ecology
and Management

Forest Ecology and Management 260 (2010) 87–95

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Differential effects of vegetation restoration in Mediterranean abandoned cropland by secondary succession and pine plantations on bird assemblages

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ARTICLE INFO

Article history:
Received 22 February 2010
Received in revised form 30 March 2010
Accepted 1 April 2010

Keywords:
Bird composition
Conservation
Habitat breadth
Regional avifauna
Species richness
Vegetation complexity

ABSTRACT

Two contrasting trajectories for vegetation restoration in agricultural landscapes are secondary succession following cropland abandonment that can regenerate woodlands (passive restoration) and conversion of cropland to tree plantations (active restoration), which have mostly focused on pine species in the Mediterranean Basin. We compared the effects of these two contrasting trajectories of vegetation restoration on bird assemblages in central Spain. Vegetation structure differed in the two restoration trajectories, pine plantations attaining higher tree cover and height (31% and 4.1 m, respectively) but lower strata complexity than secondary shrubland and holm oak woodland (which attained 10% and 1.4 m of tree cover and height, respectively). Bird species richness differed in stands under active or passive restoration trajectories, the former collecting a higher total number of species (4.2 species per 0.78 ha plot) than the latter (3.5 species per plot). The number of forest species increased with vegetation maturity in both restoration trajectories, but especially in stands under active restoration. The occurrence of woodland generalist species increased and of species inhabiting open habitats decreased in actively restored stands, being some of these latter species of high conservation priority in the European context but relatively common at the regional level. Bird species inhabiting pine plantations had broader habitat breadth at the regional level than those inhabiting secondary shrublands and woodlands. Maximum regional density did not differ between both restoration trajectories, but it increased with development of the herbaceous layer only at the secondary succession trajectory. The relative importance of species of European biogeographic origin was higher in mature pine plantations (58.9% of total bird abundance) than in mature holm oak woodlands (34.4%), whereas that of Mediterranean species was considerably higher in the latter (40.1%) than in the former (20%). Bird assemblages of relatively small patches of pine plantations are unable to reflect the regional avifauna, in contrast with the relationships between local and regional assemblage characteristics that can be found in isolated natural forests. We conclude that programs of vegetation restoration should base upon a range of approaches that include passive restoration, active restoration with a variety of tree and shrub species, and mixed models to conciliate agricultural production, vegetation restoration and conservation of target species.

1. Introduction

The structural complexity of vegetation is a major factor influencing bird communities, including their characteristics of species composition, diversity, and local abundance (Wiens, 1989). Within a particular region or landscape, human activities may profoundly modify land cover and vegetation structure and, consequently, may affect the composition and abundance of bird species (Blondel and Aronson, 1999; Heikkinen et al., 2004). For instance, large tracts of cropland have been abandoned or reforested in the world in recent decades, with noticeable effects on biological communities (Poschlod et al., 2005; Rey Benayas et al., 2007; Gómez-Aparicio et al., 2009).

Agricultural intensification and deforestation in order to create farmland can occur alongside extensive farmland abandonment which, in turn, can lead to succession back to the forest (Rey Benayas et al., 2008). Secondary succession is usually rapid in high productivity environments such as the tropics (Muñiz et al., 2006), but slow in low productivity environments such as Mediterranean areas (Bonet and Pausas, 2004). Subsidies from the Agrarian Common Policy scheme of the European Union to land owners have motivated the conversion of cropland to tree plantations. Tree plantations in dry Mediterranean regions have mostly focused on pine species, though other species such as exotic *Eucalyptus* spp. and endemic *Quercus* species have been also widely used (Reino et al., 2009). This practice allows former croplands to present more tree

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doi:10.1016/j.foreco.2010.04.004

cover than if a secondary succession leading to natural maquis or broad-leaved woodland had occurred during a similar period of time.

Habitat changes induced by land abandonment have been demonstrated to determine bird distribution patterns in large areas of the Mediterranean Basin (Preiss et al., 1997; Sirami et al., 2007, 2008; Vallecillo et al., 2008). The Mediterranean region is one of the most altered hotspots by human activities in the world. Recent changes in land use/land-cover patterns usually imply increases in forests (especially in mountain areas), and marked decreases in pasturelands and extensively cultivated areas, that are associated with increases in forest birds (e.g., Falcucci et al., 2007). Landscape changes induced by land abandonment mainly favor the short-term development of shrubland, and may potentially increase the range of potential habitats used by threatened open habitat bird species at the landscape scale. On the other hand, forest bird species could not recognize young woodland habitat patches embedded within unsuitable habitat (e.g., arable crops) as favorable environments (Virkkala et al., 2004). Thus, the distribution of woodland bird species will be mainly determined by their ability to respond to landscape changes and to colonize new habitats generated by secondary succession or tree plantations.

Increasing evidence suggests that tree plantations can support some native biodiversity and may even provide occasional habitat for vulnerable species, contributing to biodiversity conservation (Hartley, 2002; Lindenmayer and Hobbs, 2004). Nevertheless, plantations usually support modified assemblages than those found in natural habitats (Donald, 2004), and bird species richness may be reduced when natural forests are replaced by plantations. Moreover, the assemblages in plantations generally hold more species of lower conservation concern than forests; for example, Sirami et al. (2007) found that as most species of high conservation profile in the Mediterranean are tied to open or to heterogeneous transitional habitats, changes in vegetation structure linked to land abandonment and tree plantations raise questions concerning their persistence in the future. Patch size of tree plantations also exerts a prominent role in woodland species occurrence. Thus, Díaz et al. (1998) found that fragment size accounted for ca. 70% of the variation in forest bird species of pine plantations in Spanish Mediterranean plateaux, and Brotons and Herrando (2001) found that most of the woodland bird species analyzed in the north-western Mediterranean Basin were influenced by the spatial arrangement of forest fragments, especially size but also by distance to corridors and to large continuous forest habitats. Decreases in the number of species in small woodland fragments may be explained according to the loss of habitat (e.g., random sample hypothesis, Connor and McCoy, 1979) and to the indirect effects of fragmentation related to increased isolation or an increase in edge area (van Dorp and Opdam, 1987; Opdam, 1991).

Changes in bird diversity induced by land abandonment or tree plantations are dependent as well on the position of the study region within a biogeographical context and on the biogeographic origin of species. Suárez-Seoane et al. (2002) found, at the boundary of the Mediterranean and Eurosiberian regions in northern Spain, that avian diversity increased with the vegetation successional gradient for Eurosiberian birds but not for Mediterranean species during the breeding season. Eurosiberian birds showed a preference for more wooded habitats whereas Mediterranean birds preferred open habitats and shrubland. Similarly, Sirami et al. (2008) found in eight localities of the north-western Mediterranean Basin subjected to widespread land abandonment that woodland and shrubland resident species showed the strongest increase, especially those with a northern distribution, whereas migrants significantly decreased, especially farmland species with a narrow habitat breadth.

In this study, we compared how two contrasting approaches of revegetation of abandoned cropland in a Mediterranean system, namely passive vegetation restoration or secondary succession and active vegetation restoration or tree plantations, affect bird communities. These two contrasting trajectories of vegetation restoration depart from recently abandoned cropland. Our main objective was to ascertain the effects of both restoration trajectories on bird communities in agricultural landscapes by surveying bird species and vegetation structure of stands under secondary succession or planted with coniferous trees in central Spain. This study represents a direct comparison of the effects of both types of restoration trajectories on bird communities. We hypothesized that active restoration may negatively affect species that are characteristic of open habitats and that portrait high conservation value in Europe, as reforestation with pines creates a vegetation structure that is different from that present in natural Mediterranean woodlands. We also studied whether the restored vegetation under these two contrasting trajectories converge in their bird communities. These issues are relevant for management of agricultural landscapes in a time when a variety of ecosystem goods and services, and not just food and fiber production, are demanded from agrosystems. The results of this study may thus provide useful guidelines to conciliate agricultural production, restoration of native woodlands and bird conservation.

2. Methods

2.1. Study area

We surveyed bird communities in a ca. 6000 km^2 area located in central Spain. Extreme coordinates for the area are 41°00′N (North), 39°54′N (South), 3°46′W (West) and 2°51′W (East). Altitude ranges between 631 and 1008 m a.s.l. Climate in this region is continental Mediterranean, with cold winters and warm dry summers. Annual precipitation ranges between 436 mm in the lowest southern part and 598 mm in the highest northern part, and mean annual temperature between 13 and 11 °C, respectively. This region is included in the Mesomediterranean bioclimatic domain (Rivas-Martínez, 1981). Bedrock is heterogeneous with dominance of chalkstone and some extents of gypsum, granite and sandstone.

The mosaic of natural, semi-natural, introduced, and crop vegetation in the area is a result of thousands of years of human exploitation. Natural vegetation chiefly consists of evergreen forests dominated by holm oak, *Quercus rotundifolia*. The degradation of these forests has led to more open woodland dominated by *Q. rotundifolia*, *Juniperus oxycedrus*, or *Quercus coccifera* or to shrubland dominated by *Cistus ladanifer*, *Retama sphaerocarpa*, camephytes such as *Thymus* and *Lavandula* species, and herbs (e.g., *Stipa* spp.). Large extents of land were reforested with pine species (*Pinus halepensis* and *Pinus pinea*) after the 1950s and the eldest pine plantations are now semi-natural forests (Peñuelas and Ocaña, 1996). Following subsidies from the European Union, some cropland area was planted almost entirely with *P. halepensis* after 1993. Thus, most afforested abandoned cropland ranges between 3 and 15 years in age at the time we surveyed bird communities. The natural or semi-natural vegetation and pine plantations intermingle with farmland mostly consisting of rain-fed cereals and recently abandoned (<4 years old) cropland under secondary succession.

2.2. Bird census

Bird censuses were carried out during the breeding season (April 28th to June 1st) of two consecutive years (2008–2009) by means of single-visit point-counts (Bibby et al., 2000), ten minutes long each, recording all birds heard or seen within a 50-m radius plot. Overflying birds were not considered. The censuses were conducted by the same two well trained field technicians on windless and rainless days, between sunrise and 11 h GMT in the morning. Point counts do not provide absolute densities, but relative abundances. Nevertheless, the small area covered by the plots (0.78 ha), and the relatively long time devoted to bird counts, maximizes the detection probability of species and, thus, the accurate estimations of their abundance (Shiu and Lee, 2003).

Prior to sampling, we first explored the entire territory by means of aerial photographs and Google Earth®, and then visited the potential survey localities to locate the census plots. A total number of 152 census plots were obtained in 48 localities distributed throughout the study area in an attempt to sample the whole availability of habitats and the altitude gradient (every plot was censused during only one year to maximize a wide regional coverage). Of the 152 plots, 62 were located in stands under woodland secondary succession, 75 in pine plantation stands, and 15 in recently (<4 years) abandoned cropland stands. Censuses of the different considered habitats were spanned throughout the study period, avoiding censusing certain habitats in only one year. We did not observe any clear inter-annual variation in bird abundance of the study species, so we pooled all the censuses obtained in both years. The census plots were geo-referenced with a portable GPS and separated at least 200 m from each other. They were located in order to include homogeneous habitat types of the study area. These main habitat types were abandoned cropland, pastureland, camephyte shrubland, shrubland (mainly of genus *Cistus* and *Genista*), several stages of holm oak succession to mature stands, and a range of afforested croplands with pines (from seedlings to pine stands >20 years old). These habitat types were used as a guideline to select the survey localities.

2.3. Vegetation structure and NDVI

Vegetation structure was sampled within a radius of 25-m centred in each census plot, which was previously defined considering habitat homogeneity. This sampling was carried out at the end of the bird census. We estimated by eye, after training, some structural features of the habitat: percentage cover of bare soil, herbs, chamaephytes, shrubs and trees, average height of chamaephytes, shrubs and trees, and number of trunks 10–20, 21–40 and >40 cm in diameter at breast height or dbh (Table 1). Vegetation cover was estimated according to the following percentage classes: 1 (0%), 2 (0.1%), 3 (0.5%), 4 (1%), 5 (1–5%), 6 (5–12.5%), 7 (12.5–25%), 8 (25–50%), 9 (50–75%), 10 (75–90%), and 11 (>90%); we used the median values of these categories in data analyses.

Finally, we also used a normalized difference vegetation index (NDVI) as a radiometric index of photosynthetic activity (the larger the value, the more vigorous vegetation). Raw data used to calculate this index were ten-day synthesis at 1 km^2 spatial resolution captured by the MODIS Terra sensor (https://wist.echo.nasa.gov/api/) for April–June of years 2006, 2007 and 2008. For each census plot we assigned the maximum NDVI figure of the nine (3 months × 3 years) NDVI values recorded.

2.4. Species characteristics

Regional patterns of distribution–abundance of the bird species detected in the 152 point counts were summarized according to maximum density and habitat breadth of species in the biogeographic region where the study area is included (Central Spain Mesomediterranean region).

We estimated the maximum regional density (birds/km^2) recorded in 13 major habitat types of the study region as a measure of the maximum ecological abundance that a species can attain in its most favorable environment. These 13 major environments were established considering vegetation structure, floristic composition and human impact and account for more than 95% of the surface of the whole study area. They were the following: two types of urban environments (according to building height and density), non-irrigated arable crops, irrigated arable crops, mixed orchards, vineyards, olive plantations, two types of shrubland (according to shrub height and density), pasturelands, pinewoods, deciduous woodlands and holm oak woodlands. The data base for this analysis was obtained from the Spanish SACRE program (monitoring of common breeding birds in Spain), using 3417 five-minute point-counts censused in years 2004, 2005 and 2006, and distributed over the study area. Absolute densities for this data base were obtained using detectability provided by Carrascal and Palomino (2008) of the same census program.

Regional habitat breadth of species in the above mentioned 13 major habitat types was calculated following Levins' (1968) index divided by the number of habitat categories:

$$HB = \frac{[(\Sigma pi^2) - 1]}{13}$$

where *pi* is the proportion of the density for each species measured in the habitat *i* (dividing density in habitat *i* by the sum of all maximum densities recorded in the 13 habitat categories). This index ranges between 1 (evenly distributed across the 13 habitats) and 1/13 (only present in one habitat).

Bird species were included into five ornitogeographical groups according to Voous (1960): Holarctic–Palearctic, European (*sensu lato*), Mediterranean (*sensu lato*), and other two minor and rare groups in the study area (Ethiopic, and Old World).

Finally, we also looked at the relative abundances (average bird counts per census plot) of bird species in recently abandoned cropland stands and in the most mature holm oak woodland (i.e.,

Table 1
Structural characteristics of census plots in two contrasting trajectories of vegetation restoration in agricultural landscapes of Central Spain. Mean, ranges (min–max) and *P*-value according to Mann–Whitney tests for each variable are reported.

	Passive restoration (secondary succession; *n* = 62)	Active restoration (pine plantations; *n* = 75)	*P*
NDVI	0.50 (0.29–0.65)	0.48 (0.27–0.67)	0.216
Bare soil cover (%)	32 (0–62)	57 (0–95)	<0.0001
Herbaceous layer cover (%)	23 (0–95)	22 (0–95)	0.859
Chamaephyte cover (%)	14 (0–82)	10 (0–62)	0.013
Shrub cover (%)	27 (0–62)	13 (0–82)	<0.0001
Tree cover (%)	10 (0–62)	31 (0–82)	<0.0001
Mean chamaephyte height (m)	0.24 (0–0.7)	0.13 (0–0.5)	0.002
Mean shrub height (m)	1.2 (0–2.8)	1.0 (0–2.8)	0.163
Mean tree height (m)	1.4 (0–6)	4.1 (0–12)	0.0001
No. trunks 10–20 cm dbh	72 (0–781)	44 (0–184)	0.002
No. trunks 21–40 cm dbh	2.6 (0–38)	5.4 (0–59)	0.03
No. trunks > 40 cm dbh	0.2 (0–13)	0.5 (0–18)	0.809

corresponding to secondary succession) and pine plantation stands (15 stands of each trajectory).

2.5. Data analyses

Bird species richness was estimated as the total number of species detected in each census plot. Bird species composition was summarized by means of a Principal Coordinate Analysis (PCORD) on presence–absence data of the most common bird species (i.e., 19 species present in more than 5% of the census plots). Only the first component of the compositional gradient was considered in further analyses.

The average of the maximum regional density and of the regional habitat breadth in the study region of bird species in each census plot was calculated by means of the weighted averages of these figures for each species, using species counts in each plot as weights.

The relationships between the response variables (bird species richness, assemblage composition, and weighted averages of maximum regional density—in logarithm- and regional habitat breadth) and vegetation structure variables (predictors) were analyzed by means of Partial Least Squares Regressions (hereafter PLSR; Swold et al., 2001; Tobias, 2003), using census plots as sample units. This statistical tool is an extension of multiple regression analysis where associations are established with factors extracted from predictor variables that maximize the explained variance in the dependent variable. These factors are defined as a linear combination of independent variables, so the original multidimensionality is reduced to a lower number of orthogonal factors to detect structure in the relationships between predictor variables and between these factors and the response variable. The extracted factors account for successively lower proportions of original variance. The relative contribution of each variable to the derived factors was calculated by means of the square of predictor weights. Results obtained with PLSR are similar to those from conventional multiple regression techniques; however, it is extremely robust to the effects of sample size and degree of correlation between predictor variables, which makes PLSR especially useful when sample size is low and in cases of severe multicollinearity (Carrascal et al., 2009).

One-way ANCOVAs were then used to test whether the response variables differed between passive (i.e., woodland secondary succession) or active (i.e., pine plantations) restoration trajectories (fixed factor) while controlling for vegetation structure of the census plots using the scores of the first PLSR axis as covariate. The interaction term vegetation structure (i.e., PLSR scores) *x* type of restoration trajectory was also estimated to explore possible differences between restoration trajectories in the avian response to vegetation structure. Residuals of PLSR and ANCOVA models were checked to fulfill normality.

3. Results

3.1. Vegetation structure

Most variables of vegetation structure at census plots differed in the two contrasting trajectories of vegetation restoration, i.e., secondary succession and pine plantations (Table 1). There was a larger development of the tree layer and more amount of bare soil in the pine plantations than in the secondary shrubland and holm oak woodlands. However, understory layers attained higher cover values in the latter. NDVI and cover of the herbaceous layer were similar at both restoration trajectories. Most mature woodland stands averaged a tree height of 4 m and a tree cover of 45%, whereas these structural variables averaged 9.2 m and 57%, respectively, in the most mature pine plantations.

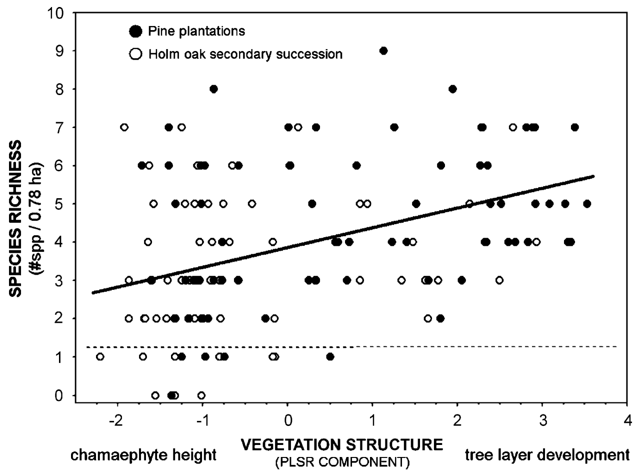

Fig. 1. Relationship between bird species richness and a vegetation structure PLSR component (positively related to tree layer development and negatively associated with camephyte height; see Table 2) in the holm oak secondary succession trajectory (open circles) and pine plantation trajectory (solid symbols). The horizontal dashed line represents the average species richness in recently abandoned croplands ($n = 15$).

3.2. Effects of vegetation restoration on bird species richness and composition

3.2.1. Species richness

The PLSR carried out with the 152 census plots provided a first component explaining 20.6% of variance in bird species richness (Table 2). This component related species richness positively to tree cover and height and to the number of thin and medium-sized trunks (10–40 cm dbh), and negatively to chamaephyte height (Table 2). Thus, bird species richness increased with development of the tree layer (Fig. 1).

An ANCOVA model performed with species richness as the response variable, type of restoration as categorical factor, and the scores of the first PLSR component of vegetation structure variables as covariate, showed that species richness was significantly higher at the active restoration trajectory than at the passive restoration trajectory ($F_{1,134} = 4.28$, $P = 0.04$). The adjusted means (controlling for the PLSR component) were 4.2 species per 0.78 ha plot in pine plantations and 3.5 species per plot in secondary shrublands and woodlands (Fig. 2A). The interaction term vegetation structure *x* type of restoration trajectory was not significant ($F_{1,133} = 0.47$, $P = 0.496$).

3.2.2. Species composition

The principal coordinate analysis (PCORD) with species occurrence in the 152 plots provided a first composition component strongly and positively correlated with the presence of generalist bird species preferring arboreal habitats (*Fringilla coelebs*, *Serinus serinus*, *Parus major*, *Cyanistes caeruleus*, *Carduelis chloris* and *Carduelis carduelis*), and negatively correlated with the presence of open habitat species (*Sylvia melanocephala*, *Sylvia undata*, *Alectoris rufa*, *Emberiza calandra* and *Galerida cristata*). The variation explained by this component was 18.6%, and it was associated with the dominant, more widely distributed species.

The PLSR analysis accounted for 58.6% of inter-plot variation in bird species composition. The PLSR component was strongly and positively related to tree layer development (tree cover and average height and density of thin and medium sized trunks) and negatively associated with development of the chamaephyte layer (Table 2).

The effect of restoration trajectory significantly influenced bird species composition (different slopes ANCOVA, $F_{1,133} = 5.29$,

Table 2
Predictor weights of the four Partial Least Squares Regression (PLSR) analyses explaining the relationship between species richness, a component of species composition, maximum regional density, and regional habitat breadth of birds (response variables) and structural features of vegetation (predictor variables) in stands of Central Spain under either passive or active restoration trajectories. Predictor weights represent the contribution of each vegetation variable to the PLSR axis. Predictor weights explaining more than 5% of the total variance in each response variable are shown in bold type.

Predictor variables	Species richness	Species composition	Maximum regional density	Regional habitat breadth
NDVI (0–255)	0.16	0.13	−0.14	−**0.35**
Bare soil cover (%)	0.09	0.20	0.11	**0.29**
Herbaceous layer cover (%)	−0.16	−0.03	**0.63**	0.20
Chamaephyte cover (%)	0.10	−0.16	−**0.44**	0.14
Shrub cover (%)	0.02	−0.20	−**0.52**	−**0.62**
Tree cover (%)	**0.61**	**0.57**	0.05	−0.10
Mean chamaephyte height (m)	−**0.25**	−**0.25**	0.04	−0.00
Mean shrub height (m)	0.05	−0.07	0.08	−**0.39**
Mean tree height (m)	**0.60**	**0.56**	0.06	−**0.32**
No. trunks 10–20 cm dbh	**0.28**	**0.25**	−0.20	−0.00
No. trunks 21–40 cm dbh	**0.25**	**0.31**	0.05	−**0.23**
No. trunks > 40 cm dbh	−0.03	0.06	0.22	−0.21
%Variance accounted for	20.6	58.6	12.2	22.8

$P = 0.023$); the occurrence of generalist woodland bird species was higher in pine plantations than in secondary shrublands and woodlands (Fig. 2B). The interaction term vegetation structure *x* type of restoration trajectory revealed a significant inter-plot variation in bird species composition ($F_{1,133} = 6.26$, $P = 0.013$) with development of the tree layer, i.e., stands under active restoration showed a strongest association between species composition and habitat maturity. Generalist bird species preferring arboreal habitats had a higher occurrence in pine plantations than in secondary shrublands and woodlands (Fig. 3).

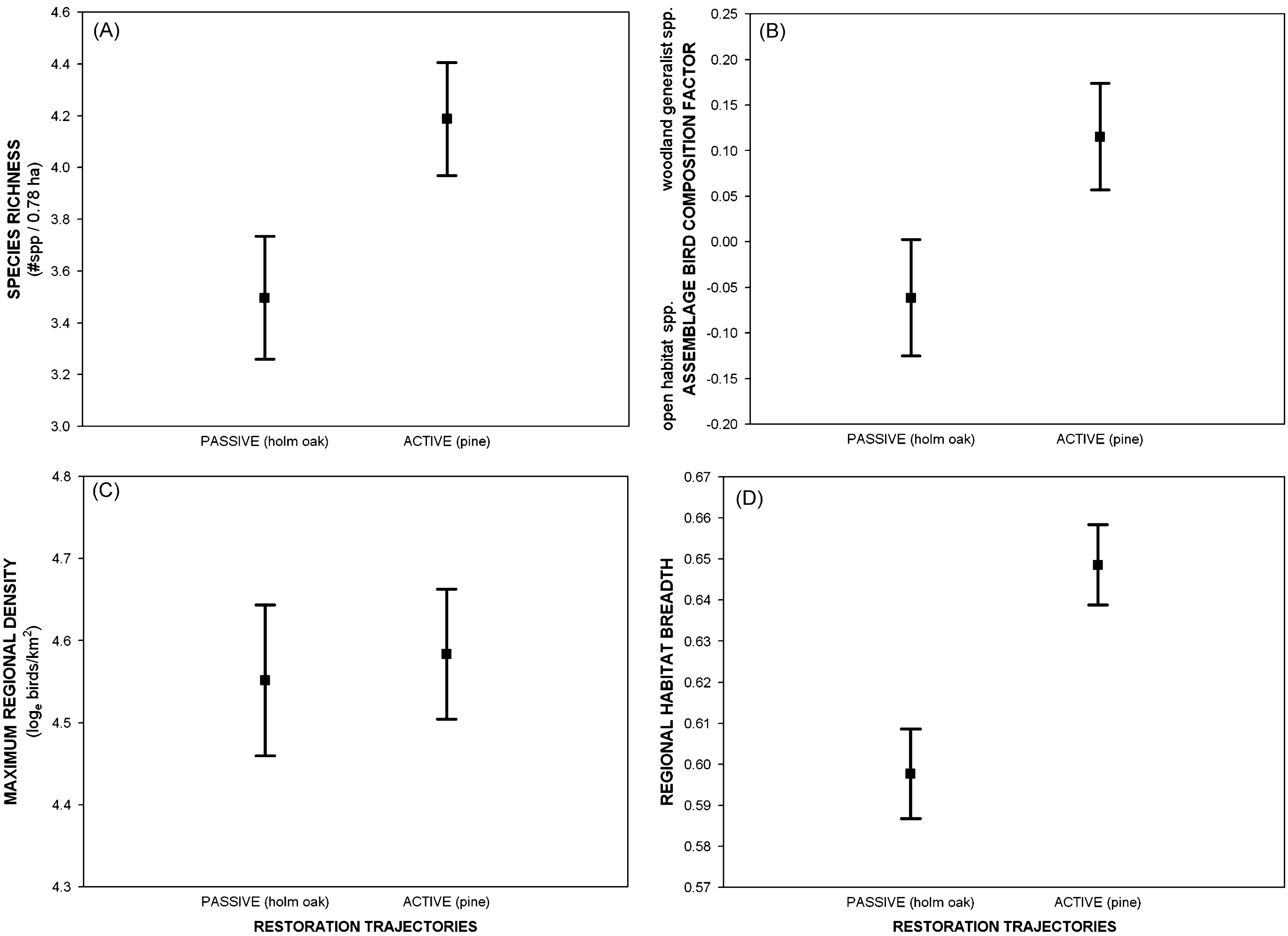

Fig. 2. Bird species richness (A), composition (B; principal coordinate component), maximum regional density (C) and regional habitat breadth (D) of bird assemblages in stands of Central Spain in the holm oak secondary succession trajectory and pine plantation trajectory. Bars denote adjusted means ± one standard error from GLMs including the PLSR vegetation component (see Section 2).

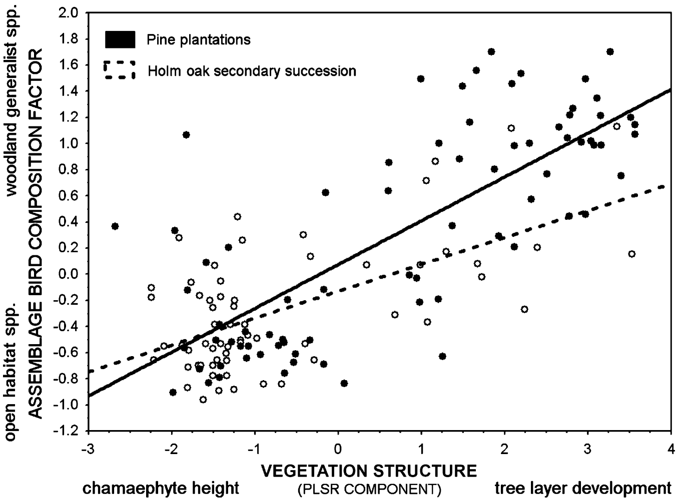

Fig. 3. Relationship between a principal coordinate component of bird species composition (opposing woodland generalists to open habitat bird species) and a vegetation structure PLSR component (positively related to tree layer development and negatively associated with camephyte height; see Table 2) in the holm oak secondary succession trajectory (open circles and dashed line) or pine plantation trajectory (solid symbols and continuous lines).

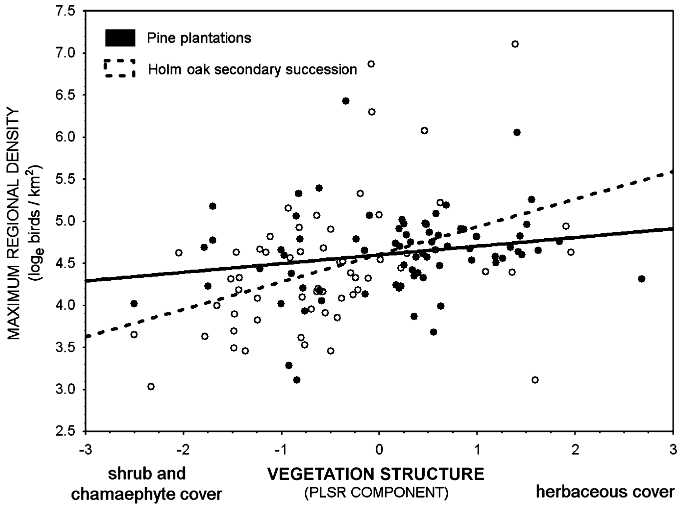

Fig. 4. Relationship between maximum regional density of bird assemblages and a vegetation structure PLSR component (increase in herbaceous cover with decreasing cover of camephyte and shrubs; see Table 2) in the holm oak secondary succession trajectory (open circles and dashed line) or pine plantation trajectory (solid symbols and continuous lines).

3.3. Effects of vegetation restoration on distribution–abundance features of bird species

3.3.1. Maximum regional density

A PLSR generated a component explaining 12.2% of variance in the maximum regional density of birds. Bird assemblages inhabiting areas with a well developed herbaceous layer and a low cover of camephytes and shrubs, irrespective of the tree layer development (see the very low weights of vegetation variables describing the tree layer in Table 2), were dominated by species which attained highest maximum density at the regional level.

An ANCOVA model provided a significant interaction term vegetation structure *x* type of restoration trajectory ($F_{1,129}$ = 4.11, P = 0.045; four census plots were treated as missing values because no species were recorded during bird censuses, and thus a weighted averaged by bird counts made no sense). Maximum regional density did not differ between both restoration trajectories (different slopes ANCOVA, $F_{1,129}$ = 0.004, P = 0.948; Fig. 2C). The slope of the regression between maximum regional density and the scores of the PLSR component was only significantly different from zero in the case of stands under passive restoration (secondary succession slope = 0.33, P < 0.001), but not in stands under active restoration (pine plantation's slope = 0.10, P = 0.159, Fig. 4). Thus, local occurrence of bird species that were very abundant in their preferred habitats at the regional scale was negatively linked to the development of the camephyte–shrub layer and increased with development of the herbaceous layer only at the secondary succession trajectory. Maximum regional density of each species is reported in Appendix A.

3.3.2. Regional habitat breadth

A PLSR analysis generated a vegetation structure component accounting for 22.8% of variance in regional habitat breadth of bird species occurring in census plots. Regional habitat breadth was negatively related to NDVI, shrub layer development (vegetation cover and height), and tree height and density of medium-sized trunks; Table 2). That is to say, habitat generalists at the regional scale are mainly linked to relatively low biomass habitats, avoiding more vegetated areas covered with growing vegetation generated by secondary succession or pine plantations.

An ANCOVA model found marked differences between the two restoration trajectories ($F_{1,130}$ = 11.86, P < 0.001; Fig. 2D). Bird species inhabiting pine plantations had, on average, broader habitat preferences at the regional level than those inhabiting the secondary shrublands and woodlands. The interaction between vegetation structure *x* type of restoration trajectory was not significant ($F_{1,129}$ = 0.146, P = 0.703; four census plots were treated as missing values because no species were recorded during bird censuses, and thus a weighted averaged by bird counts made no sense). Regional habitat breadth of each species is reported in Appendix A.

3.4. Bird density and biogeographic origin in contrasted restoration scenarios

Average bird density was 32.3 birds/10 ha in recently abandoned cropland stands, 66.3 birds/10 ha in the 15 most mature holm oak woodland stands, and 118.3 birds/10 ha in the 15 most mature pine plantation stands that were censused (Appendix A). Bird abundance of species of European biogeographic origin attained 58.9% of total bird abundance in mature pine plantations, while these figures were lower in mature holm oak woodlands (34.4%) and recently abandoned cropland (37.8%). Conversely, the relative importance of Mediterranean species was considerably higher in mature holm oak woodlands (40.1%) than in the two other habitat types (ca. 20%). Finally, species with Holarctic–Palearctic distribution were relatively more important in recently abandoned cropland (37.2%) than in mature holm oak woodlands or pine plantations (ca. 22%).

4. Discussion

4.1. Structure of restored vegetation after cropland abandonment

The identified trajectories of vegetation restoration have led to a mosaic of small patches of semi-natural vegetation in a 'sea' of croplands in the studied area. Tree plantations focused on pine species, and thus their vegetation structure is clearly different than that of evergreen secondary shrubland and woodland dominated by *Q. rotundifolia* and accompanying species. This marked difference between the two restoration trajectories is mainly determined by the larger development of the tree layer in the pine plantations due to faster growth of pines than holm oaks (Broncano et al., 1998). However, in spite of similar "quantity of vegetation" as measured by remote sensing NDVI, vertical development of vegetation structure is clearly more complex in the studied secondary succession stands than in pine plantation stands, as understory layers attain higher cover values in the former but bare soil cover is higher and a monotonous tree crown dominates in the latter (Table 1). Other studies have reported similar results to our findings (Pausas et al., 2004; Ruiz-Jaen and Aide, 2005).

4.2. Bird species composition and habitat breadth

The effects of landscape changes on bird assemblages are the consequence of their magnitude combined with adaptations that species have been able to achieve to face with such changes during their history (see Blondel, 1990; Covas and Blondel, 1998 for forest avifauna in the Mediterranean region). We highlighted that bird species composition differs in stands under passive or active restoration trajectory, the latter collecting more species that inhabit forested habitats than the former. Conversely, pine plantations are not permeable to some Mediterranean species such as *S. melanocephala*, *S. undata*, *S. cantillans*, *Lanius senator*, and *A. rufa*, which attain highest densities in the slow growing holm oak secondary succession trajectory (Brotons and Herrando, 2001; Sirami et al., 2008; Gil-Tena et al., 2009). The degradation of evergreen forests dominated by *Q. rotundifolia* as a consequence of human activities during thousands of years has led to more open woodlands or to shrublands, and thus bird assemblages in Spanish Mediterranean forests currently present a high proportion of species that inhabit more open habitats and only a small proportion of true forest birds (Santos et al., 2002). We also found that the capacity of pine plantations to collect forest birds is more dependent on the structural characteristics of vegetation than passively restored stands. Therefore, the benefits to forest birds of pine plantations in our study area are only fulfilled by tree plantations with highly mature vegetation (i.e., the oldest ones; see Fig. 3).

High habitat breadth is frequent in species that are common and tolerate a relatively wide range of ecological conditions (Hurlbert and White, 2007; Carrascal and Seoane, 2008). Accordingly, regional habitat breadth of species in our study increases with vegetation complexity, as the vegetation of stands under passive or active forest restoration grows in the 'sea' of croplands. Only generalist woodland species, with large habitat breadth at the regional level such as *F. coelebs*, *C. carduelis*, *C. chloris*, *P. major* and *Turdus merula*, are able to occupy the small woodland stands indistinctly of the type of restoration trajectory. Conversely, more specialized forest bird species, such as *Loxia curvirostra*, *Sitta europaea*, *Periparus ater*, *Lophophanes cristatus*, *Erithacus rubecula*, and *Regulus ignicapillus* are very scarce in the surveyed woodland stands (see Appendix A), as they are restricted to mature stands in large forest tracts outside the study region (the nearest areas are located in the mountain ranges of the Supramediterranean bioclimatic region in Central Spain). These results are in agreement with previous studies (Sirami et al., 2008).

4.3. Bird species richness and regional density

Tree growth under passive or active restoration trajectory positively affected both bird species richness and regional density. The influence of the passive or active vegetation restoration after cropland abandonment in this region is consistent with the pattern of relationships between bird communities and the increase in structural complexity of growing vegetation that is observed worldwide (Wiens, 1989; Nájera and Simonetti, 2009). Nevertheless, this positive effect was considerable higher in pine plantations than in the secondary succession trajectory, and is mainly related to the ubiquitous presence of generalist woodland species in the plantations. However, Díaz et al. (1998) and Maestre and Cortina (2004) found a reduction in bird diversity in pine plantations as compared to evergreen woodlands.

The fragmented character of growing woodland patches as a result of secondary succession or pine plantations is actually constraining the increase of species richness in the breeding bird communities of the Mediterranean region (Díaz et al., 1998; Brotons and Herrando, 2001). Tellería et al. (2003) have proposed that the relationship between regional richness of forest birds and richness in fragments seem to explain why fragments in southern Europe shelter fewer species than in central and northern European latitudes. These authors have also shown that the decreased ability of southern forest fragments to sample the regional richness of forest birds could be explained as an effect of the low abundance of many species in the Mediterranean, which could depress their ability to prevent extinction in fragments by a rescue effect. In a nearby region of the Spanish plateau, Díaz et al. (1998) found that plantations smaller than 25 ha only maintained 50% of the regional pool of forest birds during the breeding season.

4.4. Biogeohraphic origin and bird species richness

The increase in species richness has a different meaning according to the biogeographic origin of bird species. Pine plantations "capture" more species with European or Euroturkestan distribution patterns (Voous, 1960) than the secondary succession trajectory, while holm oak woodlands are composed by a larger proportion of bird species with a Mediterranean distribution pattern. These differences are related to past climatic events influencing the avifauna of the western Palearctic (Blondel and Farré, 1988; Blondel and Mourer-Chauviré, 1998; Mönkkönen, 1994). In the Iberian Peninsula, the patterns of geographic distribution and environmental preferences of woodland birds reflect the distribution patterns at broader geographic scales (the southwestern Palearctic region; Carrascal and Díaz, 2003). Moreover, the single climatic variable number of cloudless days per year was the most important variable negatively affecting the geography of species richness for bird species with European and Palearctic distribution pattern, while the mountainous character of areas positively affected species richness of these ornitogeographical groups. Conversely, woodland species with core biogeographic areas located in the Mediterranean basin are more frequent in the Iberian Peninsula in warm valleys, covered with little forest extent and large extensions of wooded agricultural formations (Carrascal and Díaz, 2003; see also Moreno-Rueda and Pizarro, 2008 for the effect of temperature on these biogeographic groups of bird species). At local scales, Mediterranean bird species are restricted to the early stages of succession and are replaced by temperate forest species as succession progresses on (Preiss et al., 1997).

4.5. Conservation and concluding remarks

Habitat changes induced by cropland abandonment are expected to be critical at determining future biodiversity patterns in large areas of the Mediterranean Basin (Preiss et al., 1997; Herrando et al., 2003; Sirami et al., 2007; Vallecillo et al., 2008). These changes, may be especially detrimental for several open habitat species with declining populations at both the European (Gregory et al., 2005) and the Iberian Peninsula levels (Carrascal and Palomino, 2008; Seoane and Carrascal, 2007), which are of particular conservation concern (Tucker and Heath, 1994; BirdLife International, 2004). Thus, when pine afforestation is not possible to impede, fewer but larger afforested patches rather than numerous and smaller patches scattered across the landscape may be preferable.

We did not sample any species threatened with extinction. We sampled species such as *A. rufa* and *L. senator*, with an unfavorable conservation status in Europe, which tend to be more abundant in passively restored stands than in actively restored stands, making the habitat provided by secondary succession of importance for species conservation. Since pine plantations do not attract bird species that present high habitat breadth and density, these relatively small and new habitat patches are unable to foster the assemblages of birds that are found at a regional scale. Thus, patches of pine plantations are not similar to patches of isolated natural forests regarding the capacity to foster bird assemblages, as relationships between local and regional bird communities seem to be only observed in the latter (van Dorp and Opdam, 1987).

We identified two major trajectories of vegetation restoration in Mediterranean abandoned cropland that markedly differ in vegetation complexity and associated bird assemblages. Pine plantations increased local bird species richness as they favored several Paleartic, Holarctic and European species, which chiefly are generalist woodland species. However, they failed to capture a representative pool of species from the regional avifauna, and hence are unlikely to enhance regional biodiversity of woodland birds (Díaz et al., 1998). Secondary succession provided more favorable habitats for species of conservation concern in the European context. Since passively and actively restored stands favored different bird species, any extensive and conventional forestry based on coniferous trees are improbable to be successful in conserving bird communities that inhabit complex Mediterranean mosaics of open habitats and forest ecosystems (Artman, 2003; Carey, 2003; Thompson et al., 2003; Hagar et al., 2004). Thus, programs of vegetation restoration should base upon a range of approaches that include passive restoration, active restoration with a variety of tree and shrub species native to the particular region and mixed models such as the woodland islets in agricultural seas (Rey Benayas et al., 2008) and others (e.g., Munro, 2010), which are capable of conciliating agricultural production, vegetation restoration and conservation of target species.

Acknowledgements

We are indebted to Irene Razola and Jorge Meltzer for their assistance with bird surveying. Two anonymous reviewers improved a former version of this manuscript. This research was funded by the Spanish Ministry of Science and Education (project CGL2007-60533-BOS) and the Government of Madrid (projects S-0505/AMB/0355 and S2009AMB-1783, REMEDINAL).

Appendix A.

Average density of bird species in census plots (50 m radius; birds/10 ha). RAC: recently abandoned crops (<4 years old; $n = 15$); HOLMOAK-W: mature holm oak woodlands ($n = 22$ census plots; average tree height >3 m); PINE-P: mature pine plantations ($n = 38$; average pine height >3 m). BDP: biogeographic distribution patterns according to Voous (1960; HP: Holarctic or Palearctic; E: European or Euroturkestan; M: Mediterranean s.l.; OW: Old World; ETH: Ethiopic). DMAX: maximum density recorded at the regional level in 13 major habitat types (in bird/10 ha). HB: habitat breadth at the regional level in 13 major habitat types.

	BDP	RAC	HOLMOAK-W	PINE-P	DMAX	HB
Aegithalos caudatus	HP	0.0	2.3	6.0	4.2	0.30
Alauda arvensis	HP	3.2	0.0	0.0	0.7	0.49
Alectoris rufa	M	0.6	0.6	0.0	5.8	0.79
Carduelis cannabina	E	1.3	0.6	2.0	6.9	0.81
Carduelis carduelis	E	4.5	0.0	17.8	16.2	0.83
Carduelis chloris	E	0.0	1.2	5.7	11.3	0.69
Certhia brachydactyla	E	0.0	0.0	0.7	3.0	0.53
Columba palumbus	E	0.0	1.2	4.0	9.5	0.81
Coturnix coturnix	OW	0.6	0.0	0.0	0.3	0.52
Cuculus canorus	HP	0.0	0.0	0.3	1.1	0.54
Dendrocopos major	HP	0.0	0.6	0.7	0.2	0.45
Emberiza calandra	E	6.4	1.7	0.7	11.0	0.73
Emberiza cia	HP	0.0	0.0	0.3	1.8	0.38
Erithacus rubecula	E	0.0	0.6	0.3	3.0	0.32
Fringilla coelebs	E	0.0	8.7	28.1	10.1	0.55
Galerida cristata	HP	7.0	0.6	0.0	20.6	0.71
Galerida theklae	M	1.3	0.0	1.3	2.2	0.60
Garrulus glandarius	HP	0.0	0.0	0.3	0.8	0.47
Hirundo daurica	IA	0.0	0.6	0.0	1.4	0.73
Lanius meridionalis	M	0.0	0.6	0.0	0.6	0.63
Lanius senator	M	0.6	0.6	0.0	2.9	0.51
Loxia curvirostra	HP	0.0	0.0	1.3	0.2	0.08
Lullula arborea	E	0.0	0.6	0.3	2.6	0.38
Luscinia megarhynchos	E	0.0	1.7	0.3	8.2	0.61
Periparus ater	HP	0.0	0.0	1.7	4.3	0.24
Cyanistes caeruleus	E	0.0	4.1	2.3	7.4	0.57
Lophophanes cristatus	E	0.0	0.0	3.4	2.2	0.22
Parus major	HP	0.0	2.9	7.7	6.4	0.66
Passer domesticus	HP	0.6	0.6	0.7	180.3	0.61
Phylloscopus bonelli	E	0.0	0.0	0.7	3.3	0.26
Pica pica	HP	0.6	8.7	3.0	7.0	0.84
Picus viridis	E	0.0	0.6	0.7	0.3	0.77
Regulus ignicapillus	E	0.0	1.2	1.0	2.3	0.17
Serinus serinus	M	2.5	4.6	20.4	19.5	0.68
Sitta europaea	HP	0.0	0.0	0.3	0.3	0.26
Streptopelia turtur	E	0.0	0.6	0.0	1.9	0.56
Sturnus unicolor	M	0.0	0.0	0.3	39.7	0.85
Sylvia atricapilla	E	0.0	0.0	1.0	2.2	0.47
Sylvia cantillans	M	0.0	2.3	0.0	5.4	0.36
Sylvia melanocephala	M	2.5	15.0	1.0	6.4	0.41
Sylvia undata	M	0.0	2.9	0.3	0.4	0.66
Turdus merula	HP	0.6	0.6	3.0	8.8	0.72
Turdus viscivorus	E	0.0	0.0	0.7	0.8	0.25
Upupa epops	ETH	0.0	0.6	0.0	1.1	0.73

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